Chapter 9

SECONDARY PRODUCTION AND DECOMPOSITION

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INTRODUCTION

Mesic deciduous forests are characterized by a high net primary production (Olson, 1975; DeAngelis et al., 1981; Edwards et al., 1981; Ellenberg et al., 1986). What is the fate of this organic material? This is in essence the question raised in this chapter.

A simplified diagram of the functioning of an ecosystem is given in Fig. 9.1. The decomposition subsystem performs two major functions: mineralization of essential elements and the formation of soil organic matter (Swift et al., 1979). Important ecosystem processes involving animals and the microflora are the following: consumption of living plant tissue by phytophages; decomposition of dead organic matter by reducers; and the mineralization of dead plant material, thereby filling the pool of nutrients and recycling essential plant nutrients to the plant subsystem. There are recent excellent monographs on this subject (see, for instance, Dickinson and Pugh, 1974; Swift et al., 1979).

How should the analysis proceed? According to Phillipson (1975), complex systems, such as temperate deciduous forests, should be dissected into many relatively simple components (such as species populations) and not into few relatively complex units (such as trophic levels). The parameters of population submodels are easier to define than those of trophic level submodels. On the other hand, Swift et al. (1979) emphasized that, within the decomposition subsystem, the analysis of single-species populations is not a fruitful approach to understanding the process of decomposition. However, the trophic-level approach has also not proved possible with decomposer organisms. In the following section I try to depict ecosystem processes on the species level, as well as between larger subunits of the ecosystem "temperate deciduous forest".

UTILIZATION OF FOOD: BIOCHEMISTRY, ENERGY AND NUTRIENTS

Ecological bioenergetics

Basic introductions to this topic are monographs and reviews by Petrusewicz (1967), Petrusewicz and Macfadyen (1970), Phillipson (1970), Grodzinski et al. (1975), Heal and MacLean (1975), Brafield and Llewellyn (1982), and Wiegert and Petersen (1983).

Petrusewicz and Macfadyen (1970) introduced the widely-used equations for the partitioning of energy within an animal population:

$$MR = NU + C;$$
$$C = A + FU;$$
$$A = P + R;$$
$$P = P_g + P_r = dB + E.$$

Some of the material removed (MR) is wasted (NU = not used) and the rest is ingested (C = consumption). Part of the ingested material is assimilated (A = assimilation) and the remainder is egested as faeces (F). Urine (U) is included with the faeces (as FU-rejection, egestion) because of the practical problem of separating these two pathways of energy flow. Assimilated material is used for maintenance (R = respiration) and production (P). Production is composed of growth (P_g) and reproduction (P_r) and manifests itself in field populations by the change of biomass (dB) and

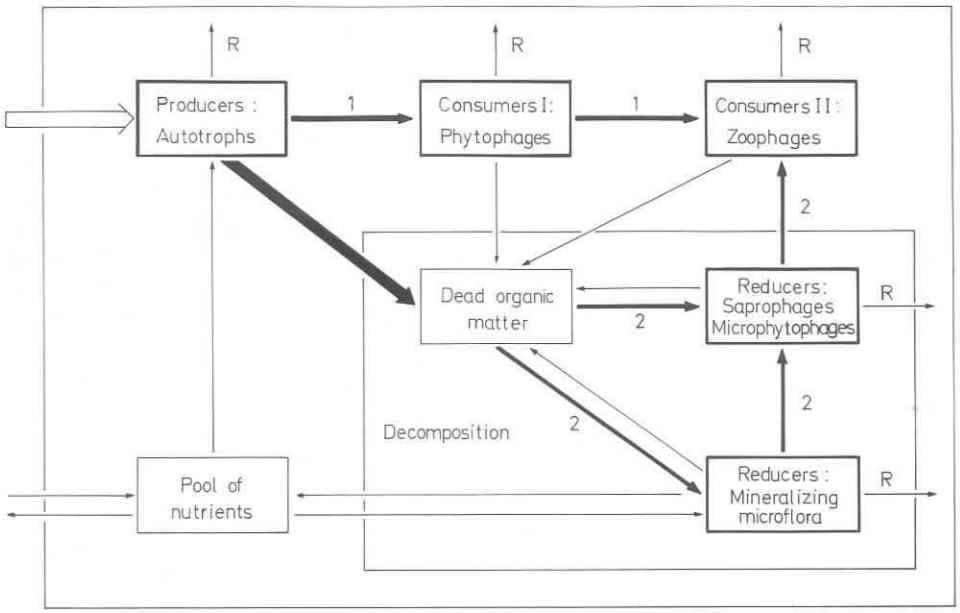

Fig. 9.1. Diagrammatic representation of energy flow and nutrient cycling in a deciduous forest. Living compartments are strongly framed. Arrows = transfer of energy and/or matter. *1* = herbivore food web; *2* = saprovore food web; *R* = respiration.

elimination (*E*: loss of biomass excluding loss of weight, for instance, by predation, death, emigration, exuviae). Heal and MacLean (1975) define "secondary production" as the sum of successive molecular reorganizations by heterotrophic organisms. There are relationships between bioenergetical parameters and attributes of the animal (for instance, weight, developmental stage, age, sex) as well as environmental conditions (for instance, temperature, food availability).

An interesting theoretical and practical problem is the weight dependence of respiration and other parameters in the equations above. In the allometric equation $R = aW^b$ (W = individual body weight), b has a value of 0.6 to 0.8 (Petrusewicz and Macfadyen, 1970; Reichle, 1971). Duncan and Klekowski (1975) cite a common value of $b = 0.75$. Petersen (1981) found that most collembolan species from a Danish beech forest had respiration–weight exponents between 0.75 and 0.85. However, the high value of $b = 0.96$ for *Tomocerus flavescens* indicates a linear relationship; Wolters (1985a) measured a value of 0.93 for the same species. The exponent clearly depends on the activity of the species in question: Wood and Lawton (1973) found values of $b = 0.54$ in very inactive Cryptostigmata and up to 1.03 in extremely active Prostigmata in the leaf-litter layer of a beechwood.

Methods

Methods for estimating the productivity of terrestrial animals are described in the books produced during the International Biological Programme (I.B.P.) [for instance, Petrusewicz and Macfadyen (1970); Phillipson (1970); Grodzinski et al. (1975)]. The empirical determination of parameters in productivity is a complex exercise, even for single-species populations with a simple life history.

All the terms can be measured for populations in the laboratory, or partly by exact monitoring of field populations. Gravimetric techniques are widely used to measure *C*, *P*, *FU*, respirometric methods are used to determine *R*, and all parameters can be estimated by tagging with radioactive material (see, for instance, Reichle and Crossley, 1965; Reichle, 1967; Wolters, 1985a). The energy content of organic material is determined by bomb calorimetry. All values are related to body biomass, which is measured directly or by regressions with linear dimensions (such as body length, body breadth, head capsule breadth).

Laboratory measurements of energy values are

not easily applied to field populations. For example, C depends on prey availability; R depends on activity of the animals; fluctuating temperatures may have different effects as compared to constant experimental temperatures; A is determined by the quality and diversity of food. Hence there may be serious sources of error in estimating energy values for animals. Some of these difficulties are discussed in the following paragraphs.

Consumption. Laboratory experiments may overestimate consumption by phytophagous insects, because weighing or measuring of consumed area does not account for the respiration of the food during the consumption period (Axelsson and Ågren, 1979). However, Waldbauer (1968) states that this error is probably negligible.

Respiration. Wightman (1981) concludes that the R term measured with a respirometer (R_m) is almost invariably less than when calculated as $C-P-FU$ ($=R_c$). It is suggested that "flask effects" are the major cause of the discrepancy between R_m and R_e, with the ratio R_c/R_m for "wild" insects as high as 2.58 on an average. However, Axelsson and Ågren (1979) supposed that the imbalance for phytophages was caused by a serious overestimate of consumption through direct weighing or measuring of consumed area, which does not account for the respiration of the food during the consumption period. Furthermore, correct values of the oxycaloric equivalent should be used (Ågren and Axelsson, 1979). McEvoy (1985) considered the commonest sources of error to be overestimation of C due to failure to correct for respiration of the diet, and underestimation of R_m caused by reduced feeding by the animals prior to and during measurement of their respiratory rate.

A key problem in respiration measurements is the influence of temperature on the respiration rate. Some authors use Q_{10} values determined in the laboratory for the animal species in question, assuming exponential temperature dependence (Q_{10} law) (see, for instance, Persson and Lohm, 1977). Generally there is agreement that Krogh's normal curve gives a good fit to the influence of temperature in respiration rate (Duncan and Klekowski, 1975; Ågren and Axelsson, 1980). The Q_{10} value may vary widely. For instance, Petersen (1981) found a range of Q_{10} from 1.9 to 3.4 for Collembola, with *Tomocerus flavescens* reaching a value as high as 5.2. Additionally, respiration measurements at constant temperatures in the laboratory do not represent the field situation with fluctuating temperatures. Albert (1983a) showed that the use of an arithmetic instead of a biological daily or monthly temperature gives slight underestimates of about 1% for respiration of two lithobiid populations in a beech-wood. However, the use of an arithmetic annual mean yields an underestimate of 14%.

Egestion. Reichle (1971) demonstrated by radioisotope measurements that "faeces" of insects and other invertebrates contain material produced through normal excretory and secretory processes, and thus the difference between C and FU does not accurately reflect digestive efficiencies. It only provides information on "net assimilation".

Another error in gravimetric analyses of faeces results from the metabolic activity of microfloral populations, which may respire a significant part of the faeces in the time period elapsing from their production to weighing.

Calculation of energy budgets

Energetics of individuals are the basis for the energy budget of populations — for instance, as "cumulative energy budget for an average individual" (Klekowski, 1970; Grimm and Funke, 1986). These values may be summed for trophic levels. Total secondary production is defined as the sum of the production of all heterotrophic organisms and includes internal production cycles because of consumption within the trophic level "secondary producers".

The calculation of energy budgets may rely partially or totally on data given in the literature, taking individual biomass as a starting point. McNeill and Lawton (1970), and in recent times Humphreys (1979), related annual production of animal populations to annual respiration. These regression equations allow the calculation of annual production from annual respiration values obtained by measurements in the laboratory, or from literature data relating R of an animal taxon to individual weight and temperature [see Persson and Lohm (1977) for further details]. Annual production and respiration values allow the calcu-

TABLE 9.1

Ecological efficiencies for terrestrial animal populations

Trophic types	Unit[a]	Ecological efficiencies[b]			
		A/C	*P/A*	*P/C*	*R/P*
Micro-organisms					
Saprotrophs	po		0.40		
Invertebrates					
Phytophages	in	0.40–0.78	0.30–0.59	0.23	
	po	0.40	0.40	0.15	
	tr	0.36–0.78	0.20–0.40	0.08–0.27	2.16–3.06
Zoophages	in	0.87	0.54	0.42	
	po	0.80	0.30		
	tr	0.47–0.92	0.10–0.37	0.34	1.70–4.18
Microphytophages	po	0.30	0.40		
Saprophages	in	0.12	0.50	0.056	
	po	0.20	0.40		
	tr	0.10–0.40	0.17–0.40	0.05–0.08	3.7–4.6
Vertebrates (Heterotherms)					
Phytophages	po	0.50	0.10		
Zoophages	in	0.81	0.62	0.50	
	po	0.80	0.10		
Vertebrates (Homoiotherms)					
Phytophages	in	0.60–0.76	0.23–0.29	0.13–0.22	
	po	0.50	0.02		
Zoophages	po	0.80	0.02		

[a]The data are based on "characteristic values" for single animal individuals (in) (from Schroeder, 1981), for populations (po) (from Heal and MacLean, 1975), and for trophic levels (tr) (from Reichle, 1977).
[b]See text.

lation of another important parameter of energetics, consumption, by using ecological efficiencies. Thus a complete energy budget of animal populations (and trophic levels) can be constructed. This approach was used by Persson et al. (1980), Axelsson et al. (1984), Grimm and Funke (1986), and Schaefer (1990), for the determination of energy budgets on the ecosystem level.

Ecological efficiencies

Ecological efficiencies are an imporant characteristic of populations of heterotrophic organisms. In Table 9.1 some values are given for *A/C* (assimilation efficiency), *P/A* (net growth efficiency, tissue growth efficiency), *P/C* (ecological growth efficiency) and *R/P* (respiratory coefficient). The estimates are in most cases rough and vary widely. This is not surprising, because populations of different species belonging to one trophic type may have special energetic attributes, and individuals within a species may have different energy requirements in different ecological situations. Many animals, especially saprophages, typically adjust their consumption rates and digestion efficiencies extensively in response to variations in the quality and quantity of food (Calow, 1977; Hassall and Rushton, 1982). For example, the digestion efficiency *A/C* of the isopod *Armadillidium vulgare* can vary from 0.1, under experimental conditions of food surplus, to 0.65 when food is more limited in the field (Hubbell et al., 1965). The assimilation efficiency of the collembolan *Tomocerus flavescens* ranged from 0.30 to 0.45, and could be raised in phases of high mobility and in periods of food shortage by lowering the gut passage rate (Wolters, 1985a).

Phytophagy

The parts of a plant have different nutritional values for phytophagous animals. The food quality

of seeds and pollen is very high; wood, however, poses many difficulties for digestion. Green plant material has an intermediate position. Green parts of herbs generally are superior to green parts of deciduous trees (Edwards and Wratten, 1980). Plant–herbivore relationships are strongly influenced by the quality and quantity of secondary plant metabolites (Harborne, 1982) (see Chapter 6) and the amount of nitrogen present in the plant tissue (Mattson, 1980). Many authors (see, for instance, Southwood, 1972; Edwards and Wratten, 1980) have emphasized that there is a nutritional hurdle for plant-feeding insects.

Energetics

Ecological efficiencies of phytophages tend to be low, especially in comparison to zoophages (cf. Table 9.1). Gastropods are an exception, as they generally have high assimilation efficiencies (Wieser, 1978). Mason (1970b) found A/C values of 0.45–0.70 for woodland snails with three field layer plants as food. Efficiencies were as follows: *Discus rotundatus* 0.45; *Trichia striolata* 0.52; *Helix aspersa* 0.54; *Oxychilus cellarius* 0.70. Extremely low assimilation efficiencies have been found for phloem-feeding Hemiptera — for instance, a value of $A/C \approx 0.1$ for the lime aphid, *Eucallipterus tiliae* (Llewellyn, 1972).

Saprophagy and microphytophagy

It is often difficult to distinguish between those soil and litter animals feeding on detritus and those selecting microflora as food (see Chapter 6). In many cases species are characterized by a mixed diet. There is even a hypothesis stating that true saprovores seem to have as their main energy source the microbial biomass on or in the dead organic matter they consume (Anderson and Bignell, 1980). This is perhaps the answer to the question, which is unresolved according to McBrayer (1973), how the "fragmenters" maintain viable populations on litter which is intrinsically low in readily available energy and essential elements. Fungi are a desirable resource, because of their energy content and the elements they contain (Martin, 1979). The same is true for bacteria and unicellular algae (Swift et al., 1979).

Utilization of dead organic matter and microfloral food

Detritus-feeding animals and microphytophages often are regarded as trophic generalists. However, this is only partly true. Which factors in the food resource are responsible for the different degrees of utilization? How are the saprophagous animals adapted to digest litter and detritus? These are major questions to be answered.

The digestive capacities of the soil and litter species are different. A crucial point is the possession of carbohydrases enabling the saprovores to digest carbohydrates such as cellulose. These enzymes are provided either by gut "symbionts" or by soil and litter microflora or are synthesized by the animals themselves. Digestion is thus performed: (1) by an animal's own enzymes (Nielsen, 1962); (2) before feeding by external enzymes provided by decomposing microfloral populations; (3) in the gut by extracellular cellulases from bacteria; (4) in the gut by bacteria or Protozoa which are subsequently digested; or (5) by means of autocoprophagy. Thus there are "true decomposers" with own carbohydrases [gastropods, some dipterous larvae, some oribatids, some millipedes, such as *Polydesmus angustus* (Beck and Friebe, 1981)], and consumers, which have extended their digestive capacities. In this sense the saprovore fauna is tightly linked to the microflora. Gist and Crossley (1975a) and Swift et al. (1979) regarded the microflora plus substrate as an "external rumen": by successive ingestion and reingestion of organic litter the saprophagous animals derive an energy and nutrient supply from the substrate which they cannot digest themselves (Crossley, 1977). According to a hypothesis of Martin (1979, 1984) digestion of litter material in the guts of arthropods may occur because of the acquisition of fungal enzymes.

There is much experimental work on **digestion** in the saprovore food web. Reyes and Tiedje (1976) demonstrated that microbial biomass (*Flavobacterium*, *Pseudomonas*) was digested by woodlice (*Trachelipus rathkei*), especially under nutrient-limiting conditions. Normally the relative contribution of gut microbial activities to organic-matter digestion by this species was minimal (Reyes and Tiedje, 1973). A fairly rich bacterial flora, active in the decomposition of carbohydrates and protein, was isolated from the alimentary canal of speci-

mens of the oribatid mite *Achipteria coleoptrata* (Stefaniak and Seniczak, 1976). In many cases it is difficult to decide whether digestive enzymes are produced by the animals themselves or by microfloral populations in the gut or outside the gut. Important enzymes are carbohydrases (esp. cellulase), trehalases (for the digestion of fungal material) and peroxidases (for degradation of aromatic compounds). According to Hartenstein (1982), earthworms have significant amounts of cellulase (being significantly more important than in isopods or diplopods) and peroxidase (suggesting a dominant role for earthworms in the condensation stage of the humification process). I will give only two examples of more detailed studies.

The isopod *Oniscus asellus* can degrade radioactively-labelled cinnamic acid, phenol and quinic acid. This animal can thus take part in the degradation of secondary plant substances in the soil, and may be involved in lignin degradation (Neuhauser and Hartenstein, 1976). It is not known whether the test compounds were metabolized by isopod oxidase or by internal microbes. In a more recent study, Kaplan and Hartenstein (1978) examined twelve species of soil macroinvertebrates for activities of mono-oxygenases and dioxygenases, which are prerequisites for the degradation of aromatic compounds. Only homogentisate oxygenase (a dioxygenase) was detected, and it was present in only four species of earthworms. The apparent absence of mono- and dioxygenase activity in *O. asellus* and other species (except the Lumbricidae), and the absence of pyrocatechase, metapyrocatechase, procatechuic, 3,4- and 4,5-dioxygenases in eurykaryotes other than fungi, suggest that for all these soil macroinvertebrates scission of aromatic rings is attributable to micro-organisms. Zinkler (1971) found saccharase, maltase and α-amylase as enzymes in microphytic feeders among Collembola and Oribatei performed preferential hydrolysis only of intercellular compounds of the microflora. On the other hand macrophytophagous oribatid mites are able to attack structural polysaccharides by carboxymethylcellulase, xylanase and pectinase.

Apparently the function of **autocoprophagy** — the habit of reingesting faecal material — is the conversion of unavailable substrate to digestible microbial protoplasm and to partly degraded plant compounds. Autocoprophagous invertebrates are found among the Isopoda (Wieser, 1978), Diplopoda (McBrayer, 1973) and xylophagous beetles (Mason and Odum, 1969). Hassall and Rushton (1982) observed that faeces formed a significantly greater proportion of the diet when individuals of *Porcellio scaber* were fed freshly fallen litter of *Betula pendula* rather than decayed litter. They concluded that enhanced microbial activity in the faeces increased their nutrient status in such a way that some coprophagy was necessary in order to optimize overall nutrient uptake, and that the ability to vary the extent to which faeces are recycled in response to differences in food quality is important in that it introduces greater flexibility into the feeding strategies of these generalist macro-decomposers. Hassall and Rushton (1985) examined preference by *P. scaber* for reingesting faeces of different age. Faeces that had decayed for two to three weeks were preferred to recently deposited ones. Hence coprophagous behaviour evolved as a way of utilizing the activities of microorganisms in an "external rumen" rather than as a form of "refection" to aid absorption of materials that had been digested posterior to the main absorptive regions of the alimentary canal. McBrayer (1973) found that the litter-feeding millipede *Apheloria montana* showed small weight increases if it was solely fed on leaf litter (1.1% in 30 days). A second group of animals, which were allowed access to their faeces, increased their ingestion rates by more than 60% and their growth rate by 16% over the controls.

Energetics

According to radionuclide studies in a *Liriodendron* forest, surface-feeding saprophages consumed $1.0 \pm 0.4\%$ of their dry body weight per day, and the fungivores of the soil ingested fungal material at an average daily feeding rate of $7.1 \pm 2.4\%$ of their dry body weight (McBrayer and Reichle, 1971). Ecological efficiencies of saprophages are comparatively low (cf. Table 9.1).

There are studies demonstrating that the feeding behaviour and assimilation rates of saprophages are adapted to the microclimate, especially temperature, in their litter and soil microhabitats. The diplopod *Narceus americanus* of a mesic forest utilized assimilated energy for growth and repro-

duction only between 14 and 24°C, temperatures at which assimilated energy exceeds that required for basal metabolism (O'Neill, 1968). The litter-dwelling snail *Perforatella incarnata* ingested maximum quantities of food at 10 to 15°C in a mesic beech forest (M. Corsmann, pers. comm., 1986). For the same woodland, T. Sprengel (pers. comm., 1986) found maximum assimilation rates for the diplopods *Glomeris marginata* and *G. conspersa* at 10°C. These temperatures are typical for the litter stratum of the forest during the vegetation period.

Macrofauna. Species of Lumbricidae have different consumption rates (Piearce, 1978). *Lumbricus rubellus*, as a litter feeder, consumes 25 to 50 mg dry weight per gram of fresh weight per day, and *Aporrectodea caliginosa*, as a topsoil feeder, 40 to 80 mg g^{-1} day^{-1}. Assimilation efficiencies are low: Bolton and Phillipson (1976) found A/C to be about 0.01 for *Aporrectodea rosea*. Phillipson et al. (1978) observed a P/B ratio of 0.49 to 0.58 for the lumbricid fauna in an English mixed deciduous forest.

The assimilation efficiency of the gastropod *Discus rotundatus* on leaf litter, with a mean of 0.49 on five litter types, is higher than that shown by other invertebrate non-gastropods, probably due to the presence of gut polysaccharidases (Mason, 1970b) (see p. 179).

Isopods exhibit low assimilation efficiencies; they are generally considered to be poor exploiters of food. However, A/C ratios are reported in the literature from 0.16 (Hartenstein, 1964) to 0.70 (Reichle, 1967). Because of the generally low assimilation efficiencies, isopods are characterized by high litter feeding rates, ingesting up to 10% of their body weight daily as litter. Thus isopods accelerate the mechanical disintegration of the primary organic matter in woodlands (Wieser, 1978). According to a study by Neuhauser and Hartenstein (1978), isopods consumed about four times more leaf material per gram body weight than millipedes, which are more effective digesters.

Mesofauna. Collembolans and oribatid mites have been well studied. For forest Oribatei consumption rates vary between 1 and 15% of the dry body weight per day. Assimilation efficiencies generally exceed 0.4 in a range that spans 0.03 to 0.65. Metabolic rates are relatively low, with P/A ratios for some species exceeding 0.9 (Wallwork, 1983). However, Luxton (1981) found much lower P/A values of 0.25 to 0.65, A/C ratios between 0.5 and 0.6 and much higher variation in consumption (1–40% of dry body weight ingested per day). Range of production turnover for adults, P/B, was 1.6 to 7.5.

Testerink (1982) summarized energy data for Collembola, with A/C ratios between 0.2 to 0.7 and P/A ratios between 0.3 to 0.5. In a thorough analysis using radioactively-labelled algal food, Wolters (1985a) determined the energy budget of the epedaphic[1] forest species *Tomocerus flavescens*. The assimilation efficiency ranged from 0.34 to 0.40 (as dry weight) and from 0.30 to 0.45 (as energy units). A/C was negatively correlated with gut passage rate.

Less information is available for Enchytraeidae. Phillipson et al. (1979) found a net population production efficiency P/A of 0.32 for a mixed forest population with a production turnover (P/B) of ≈ 4.93.

Microfauna. Although there do not exist so many experimental data on the energetics of soil microfaunal groups, it appears that some of them are very important in energy flow of the total soil animal community.

Testacea have a very high rate of production turnover, with values of $P/B \approx 30$ to 100 depending on the species (Schönborn, 1982). Biomass turnover (P/B) of Protozoa in a deciduous mull forest was equally high: 43 for Testacea, 13 for naked amoebae, and 18 for flagellates (Meisterfeld, 1986).

For nematodes in an English deciduous forest, Phillipson et al. (1977) found a P/A ratio of 0.37 and a P/B ratio of 5.16.

Zoophagy

Zoophagous animals use a food resource of high quality and do not need a special set of enzymes. However, they generally have to allocate a high amount of energy to searching for prey (Brafield and Llewellyn, 1982).

Energetics

Radionuclide studies in a *Liriodendron* forest suggest that the consumption rate of predatory soil

[1]See Chapter 6.

animals of the mesofauna is less than that of fungivores and higher than that of saprovores. Larvae of Dolichopodidae, gamasine mites, Scutacaridae and other prostigmatid mites ingested $2.5 \pm 1.0\%$ of dry body weight per day (McBrayer and Reichle, 1971).

Ecological efficiencies are given in Table 9.1. The energy budgets of only a few groups have been well studied experimentally — for instance, mesostigmatid mites (Luxton, 1982), Araneida (Moulder and Reichle, 1972), Chilopoda (Albert, 1983a, 1983b), Carabidae (Thiele, 1977; Grüm, 1978), and Formicidae (for instance, Horstmann, 1982).

PROCESSES WITHIN SUBUNITS OF THE ECOSYSTEM

Main topics are energy flow and nutrient dynamics within important subsystems of the forest ecosystem.

Plant subsystem

Trees and bushes

Mean annual values of primary production for temperate deciduous forests are 1200 g m^{-2} yr^{-1}, with a range of 600 to 2500 g m^{-2} yr^{-1} (Whittaker, 1975). More data are given in DeAngelis et al. (1981). Main components of trees are stems, leaves, and roots. For a cove forest in Tennessee (U.S.A.) with a net productivity of 1300 g dry wt m^{-2} yr^{-1} for the entire tree, the percentages for the biomass components were: stem wood 33.3, stem bark 3.7, branch wood and bark 13.1, leaves 29.1, fruits and flowers 1.8, and roots 19.0% (Whittaker, 1975).

Canopy. Estimation of consumption of leaf-eating insects in forest canopies, mostly deciduous, have been obtained in connection with energy-flow and/or nutrient-cycling studies (see, for instance, Bray, 1964; Carlisle et al., 1966; Rafes, 1971; Smith, 1972; Grimm, 1973; Axelsson et al., 1974; Gosz et al., 1978; Nielsen, 1978; Phillipson and Thompson, 1983; Witkowski and Borusiewicz, 1984; Grimm and Funke, 1986; Schowalter et al., 1986). Some of these studies concern grazing by single-species outbreak populations during only part of the season, while others give figures on consumption on an annual basis without any further dimension (see Table 9.2). Reichle and Crossley (1967) and Reichle et al. (1973) used a different approach by estimating directly from feeding damage on leaves both consumption rates and total consumption for a complete season, estimating feeding on different age-classes of leaves, and relating grazing to different consumer groups. Lately, Schroeder (1978) has reported on consumption rates as well as totals for a whole season, estimated from faeces production.

Bray (1964) estimated that from 5 to 7.7% of the canopy leaf areas of *Acer*, *Fagus* and *Fraxinus* were consumed. Reichle and Crossley (1967) using tracer techniques estimated that 5.6% of leaf production in a *Liriodendron tulipifera* forest was consumed by insects. Smith (1972) observed that 4% of the leaf energy content of a hazel (*Corulus avellana*) coppice in England was consumed in 1965, but only 1.3% in 1966. Total leaf consumption by phytophages in stands of black cherry (*Prunus serotina*) in Ohio (U.S.A.) was 2.9% or 3.0% of the leaf fall for dry mass or energy, respectively (Schroeder, 1978). About 5% of the leaf fall in a German beech (*Fagus sylvatica*) forest was consumed by phytophages (Funke, 1973; Grimm and Funke, 1986). In a Danish beech forest, the apparent beech leaf consumption ranged from 7 to 20% (average 12.3%), actual removal by phyllophages was 5.7% (range 3–9%) of leaf area or 3% (range 2–5%) of annual leaf production (Nielsen, 1978). In an English beech forest, Phillipson and Thompson (1983) observed an apparent damage equivalent to 5.7% of total leaf area in one year and 4.0% in the next year. Values for the actual material removed were 3.4 to 4.0% and 2.4 to 2.7%, respectively. Phyllophagous insects of a Polish oak (*Quercus robur*)–hornbeam (*Carpinus betulus*) forest consumed 13.6 to 37.0% of the total production of oak leaves (Witkowski and Borusiewicz, 1984). These and further data (especially for single-species populations) are presented in Table 9.2.

Browse production in a Polish deciduous forest was estimated to 172 kg dry wt ha^{-1} (Bobek et al., 1979). However, only 160 kg were actually produced due to deer consumption. During the growing season roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) removed 46 kg (27%) of the browse production, of which they only consumed 19 kg. The balance of 27 kg was destroyed

TABLE 9.2

Consumption of canopy leaves by phyllophages in temperate deciduous forests

Forest type	Annual consumption (%)	Method, basis of calculation	Reference
(A) Total consumption (yr^{-1})			
Xeric *Quercus*	10.6		
Mesic *Acer–Fagus*	6.6 mean of 3 years	Leaf area	Bray (1964)
Moist *Acer–Fagus*	5.9		
Liriodendron	5.6	Leaf area	Reichle and Crossley (1967)
Liriodendron	7.7	Leaf area	Reichle et al. (1973)
	=2.6	Annual leaf production	
Corylus coppice	4 (1965); 1.3 (1966)	Leaf energy content	Smith (1972)
Fagus	5.9	Leaf biomass	Funke (1973)
Prunus	2.9	dry mass of leaf fall	Schroeder (1978)
Fagus	12.3	Leaf area	Nielsen (1978)
	=5.7	Net leaf area	
	=3	Annual leaf production	
Mixed woodland	5.7; 4.0 (2 years)	Leaf area	Phillipson and Thompson (1983)
	=3.4–4.0; 2.4–2.7	Net leaf area	
(B) Consumption by phytophagous populations (yr^{-1})			
Tortrix viridana			
Mixed woodland	2–27 (in years of defoliation)	Number of leaves	Carlisle et al. (1966)
Phytodecta pallida			
Mixed woodland	0.42 ± 0.46	Annual leaf production (energy)	Axelsson et al. (1974)
Operophthera spp.			
Mixed woodland	0.004 ± 0.006 (during fluctuation low)	Annual leaf production (energy)	Axelsson (1977)
Lepidoptera, Curculionidae			
Fagus	≈ 1	Annual leaf production	Winter (1985)

and not utilized as food. The two cervid species are the dominant herbivores in the forest with respect to biomass, but they eat only 1% of the total primary production, that of herbs included (Bobek and Perzanowski, 1984). Generally, mammals consume only a small amount of available primary production (Ryszkowski and French, 1982).

In summary, it appears that consumption rates in forest canopies are generally low. This tendency is aggravated by the fact that many herbivores feed more in shade (Funke, 1973; Nielsen and Ejlersen, 1977; Maiorana, 1981). Because shade leaves receive only a small fraction of the photosynthetically active radiation, overall decrease in the rate of photosynthesis of a tree often is negligible and does not significantly affect primary production.

However, some kinds of feeding pressure may substantially reduce tree growth. Aphids, for example, may impose a high energy drain on trees. Llewellyn (1972) found that populations of the lime aphid, *Eucallipterus tiliae*, on lime (*Tilia*) trees in Scotland consumed the equivalent of 15.4 MJ m^{-2} yr^{-1}, which is a high percentage of net primary production and considerably higher than reported for other canopy herbivores. The aphid *Macrosiphum liriodendri* consumed only 1% of annual photosynthate production of *Liriodendron tulipifera*, but an amount equivalent to 17% of the annual standing crop of foliar nitrogen (Van Hook et al., 1980). In the absence of aphids (*Drepanosiphum platanoides*), sycamore trees (*Acer pseudoplatanus*) could produce as much as 280% more stem wood (Dixon, 1971a). Sycamore produces small leaves when heavily infested with aphids in the spring. In the years when aphids are abundant in the spring, the leaves are still rich in nitrogen when they fall in autumn. Leaves infested with aphids have a net dry-matter production rate 1.7 times

greater than uninfested leaves, thus partially compensating for energy drains. Experiments on lime saplings (*Tilia vulgaris*) revealed that the roots of saplings infested with aphids (*Eucallipterus tiliae*) did not grow, leading to a reduction in overall production. Saplings infested with aphids shed their leaves earlier, the leaves were heavier per unit area and they contained more nitrogen (Dixon, 1971b). Aphid infestation in one year resulted in smaller leaves in the following year, and these leaves were darker green and had a net production 1.6 times greater than the leaves of previously uninfested saplings.

In moist climates substantial amounts of material may move from the forest canopy to the forest floor in solution or suspension (Carroll, 1979). This flow of nutrients may be influenced by phytophagous canopy populations. For instance, the through-fall precipitation was enriched by a factor of about 3 with respect to nitrogen, phosphorus and potassium in a beech stand during defoliation by the pale tussock moth *Dasychira pudibunda* (Nilsson, 1978).

Seeds. Often seed predation in the canopy is heavy. Seeds falling on the ground experience a similarly high predation pressure (see Chapter 6). Weevils of the species *Conotrachelus affinis* attacked about half of the fruits of the pignut hickory, *Carya glabra*, in an oak (*Quercus alba, rubra, velutina*)–hickory (*Carya glabra, ovata*) forest in Michigan (U.S.A.) during a 2-year study (Boucher and Sork, 1979). A similarly heavy seed-predation pressure was documented for blue jays (*Cyanocitta cristata*) transporting or eating acorns of *Quercus palustris* and other Fagaceae with small- and medium-sized nuts (Darley-Hill and Johnson, 1981).

A thorough quantitative study was made by Nielsen (1977) of beech seeds in a Danish beech forest. Annual seedfall during 1967 to 1974 represented 2 to 54 g dry wt m^{-2}, of which 5 to 20% were barren. The tortricid *Cydia fagiglandana* attacked 7 to 55% of the seeds, which is a consumption rate of 0.7 to 5.4 g dry wt m^{-2} yr^{-1} (21–154 kJ m^{-2} yr^{-1}) or 8 to 61% of the annual endosperm production (average 36%). Feeding by granivores on the seeds on the ground (as a potential food resource of 1–34 g endosperm m^{-2} yr^{-1}) was insignificant in this forest. Most of the seeds entered the detritus pathway. However, predation by small mammals may be a significant mortality factor for seeds of forest trees, especially during intermast periods (Hayward and Phillipson, 1979; Gorecki, 1984a) (see Chapter 6).

Wood. Although wood constitutes about 74% of biomass in temperate deciduous forests (Whittaker, 1975) and the rate of increment of woody biomass is high (Whittaker, 1975), there are no exact experimental, quantitative data on consumption of living wood by xylophagous animals. The "cambiophagous" and xylophagous beetles (larvae of Buprestidae, Cerambycidae and Scolytidae) consumed about 0.002% of the standing crop of a Polish oak (*Quercus robur*) forest, and 0.005% of the standing crop of a mixed pine forest (Witkowski and Borusiewicz, 1984).

Phyllosphere and phloeosphere. New (1970) demonstrated that weights of adventitious material scraped from adaxial surfaces of leaves of several common forest trees in Great Britain ranged from 1 to 25 mg dm^{-2}. On beech the maximum occurred in July, with the median value amounting to 6 mg dm^{-2}. Between 10 and 25% of the material was pollen, animal remains and other non-microbial materials. Generally, the standing crop of micro-epiphytes in forests is estimated to be 5 to 10 g m^{-2} (Carroll, 1981). In a Danish beech forest, biomass of aerobic chemi-organotrophic bacteria was determined to be about 1 g dry mass m^{-2}, with 0.12% in the phyllosphere (0.03% in the tree canopy, 0.09% in the ground vegetation: Holm and Jensen, 1972).

In old-growth coniferous forests there is evidence for a mechanism for the conservation of nutrients within the canopy involving canopy arthropods (Carroll, 1979). For example, these mechanisms involve fixation of atmospheric nitrogen by cyanophycophilous lichens, the loss of organic nitrogen from such lichens through leaching, the uptake of leached organics from dilute canopy solutions by micro-organisms and other epiphytes, and the consumption of a portion of the resulting microbial production by canopy microarthropods (Carroll, 1981). Thus, leached organics serve indirectly as a base for many canopy food chains. In contrast to coniferous woods, temperate deciduous forests, in which the leaves are shed

annually, show less evidence of nutrient uptake and release by microbial cells. However, there are situations where concentrations of macroelements in the canopy solution of the through-fall of rain may be high (Carroll, 1979): (1) aphid infestations, which are widely reported to encourage the growth of yeasts and sooty moulds on canopy surfaces coated with honey dew; (2) outbreaks of defoliating insects (Nilsson, 1978; Schroeder, 1978); (3) foliar fertilization; and (4) atmospheric pollution. These may be the resource of a temporary food web within the canopy of trees and forests.

The phloeosphere — a rather complicated subsystem in the canopy and on tree stems — may have high values of standing crop and net primary production. For *Pleurococcus* algae on the bark of European larch (*Larix decidua*) trees in a larch–beech forest, Turner (1975) calculated a value of net primary productivity (NPP) = 0.9 g dry wt m^{-2} yr^{-1} (15.5 kJ m^{-2} yr^{-1}). Total net primary productivity of all epiphytes was 1206 kJ per square metre of bark surface per year (1930 kJ per square metre of ground area per year) — that is, equivalent to about 60 g dry wt per square metre of bark, or 96 g per square metre of ground area per year (Turner, 1983a). In this larch–beech forest epiphyte herbivores, namely Collembola and Psocoptera (the latter group being of minor importance) consumed 11.0 and 8.3 kJ per square metre of bark surface in 1977 and 1978, respectively — that is only about 1% of the epiphyte material available to them. Turner (1983b) calculated the *Mesopsocus* annual production, according to the data of Broadhead and Wapshere (1966), to range from 7.1 to 38.1 kJ per square metre of ground area per year. According to a rough estimate by Wolters (1985a), the population of *Tomocerus flavescens* in a German beech-wood consumed 0.83 g of the algal dry mass growing on one beech tree during one summer.

Pike (1978) emphasized that lichens in an oak (*Quercus garryana*) woodland were not really important in above-ground mineral turnover, with a ratio between lichen turnover and leaf litter of 0.15 for biomass, 0.15 for nitrogen, 0.09 for calcium and 0.07 for magnesium. This result may underscore the relative unimportance of phloeosphere animals (with low consumption rates) in above-ground nutrient dynamics.

Roots. Studies of root biomass have been summarized in reviews by Ovington (1962), Santantonio et al. (1977) and Harris et al. (1979). The proportion of the total biomass as root organic matter decreases during forest development. In a *Liriodendron tulipifera* forest, annual net root biomass production was 9.0 t ha^{-1}, with a net annual turnover (translocation and sloughing) of equal magnitude. This value of net annual root production is 2.8 times larger than mean annual above-ground wood production (Harris et al., 1979). For temperate deciduous forests, the common assumption that below-ground primary production is a fraction of above-ground primary production proportional to biomass pool size leads to an underestimate of total annual root production. A spring–fall bimodal peak in root biomass has been revealed in some studies (beech forest: Ellenberg et al., 1986; *Liriodendron* forest: Harris et al., 1979). Fine roots are responsible for a large flux of organic matter (Harris et al., 1979). Nadelhoffer et al. (1985) reported fine-root annual turnover rates for sites in an Arboretum in Wisconsin (U.S.A.) dominated by black oak (*Quercus velutina*) of 2.19, by read oak (*Q. rubra*) of 1.94, by white oak (*Q. alba*) of 1.21, by maple (*Acer saccharum*) of 0.94 and by birch (*Betula papyrifera*) of 1.02. Fine-root production and total net primary production (in g m^{-2} yr^{-1}) were as follows: for the black oak site 591 (1694), red oak 524 (1895), white oak 413 (1498), maple 402 (1334) and birch 324 (1004). One may hypothesize that the permanent rebuilding of fine-root structure favours the exploitation of new areas of the soil (Harris et al., 1979). Furthermore, during periods unfavourable for growth (fall–winter), or when above-ground energy demands are high (spring–early summer during canopy development), root biomass is sloughed off, thereby reducing the total energy demand of the forest ecosystem. Nutrients contained in sloughed material are conserved in the soil by immobilizing microbial processes (Harris et al., 1979). In a *Liriodendron* forest, annual return of elements to the soil was three times the combined above-ground inputs (including atmospheric) for potassium, and at least 1.5 times above-ground inputs for nitrogen (Cox et al., 1978).

Thus there is a plentiful, seasonally varying resource for herbivores and saprovores present in

the root zone of trees. What is the fate of seasonal fluxes of organic matter below-ground? Estimates of total herbivory on roots do not exist. Root-feeding nematodes and various larval stages of insects (such as cicadas, beetles) might be principal consumers (Ausmus et al., 1977). In an American *Liriodendron* forest the annual root consumption by cicada larvae was calculated as 8.61 g dry wt m^{-2} or 1.14% of the average root biomass <0.5 cm diameter. Nematodes consumed 63.8 g m^{-2} yr^{-1} of roots <0.5 cm diameter, approximately 8.5% of the mean annual root mass (Ausmus et al., 1977). In a study by Cox et al. (1978), consumption of root biomass was assumed to be 10% of root detritus, a value which appears to be high for temperate deciduous forests (Ausmus et al., 1977). According to Schauermann (1977), consumption by Curculionidae was 0.1% of (above-ground) net primary production. Thus evidence points to a small absolute flux of energy through consumption of roots. Despite the obvious small absolute role of animal consumers, one should not prematurely dismiss their importance to the functioning of forest ecosystems. Schauermann (1977) regarded the curculionid beetle larvae as accelerators of the mineralization process, because of physical damages to roots and effect of their faeces on microbial decomposition. He found that 87% of energy turnover in the rhizophagous larval population occurred between August and April — a period generally coincident with high root turnover and high nutrient demand by trees.

Rhizosphere and mycorrhizae. Quantitative studies on the role of animals in energy flux and nutrient dynamics of tree rhizospheres are lacking. Bacterial effects, however, have been widely studied. In the rhizosphere asymbiotic nitrogen fixation is often higher than in the surrounding soil; ammonifying bacteria, denitrifiers and phosphate-dissolving bacteria have been reported to be more abundant in the rhizosphere; rhizosphere microorganisms can influence calcium, sulphur and phosphorus uptake, among other effects (Rovira, 1965). Coleman et al. (1984) hypothesized that pulses of root exudates stimulate microbial, especially bacterial, growth and that microfauna (mainly nematodes), which feed on the bacteria, enhance mineralization of immobilized carbon, nitrogen and phosphorus.

The mycorrhizal subsystem is vital for most woody plants (Grant and Long, 1981). This is shown by improved growth and enhanced mineral content of tree seedlings infected with mycorrhizal fungi. Understanding of the underlying mechanisms is incomplete, although phosphorus uptake has received considerable attention. Mycorrhizal roots of beech (*Fagus sylvatica*) incorporate phosphorus as phosphate at rates two to five times those of uninfected roots, most of the phosphorus accumulating as an inorganic pool within the fungal sheath, and then being transferred to the plant when external phosphorus levels are low. This improvement in phosphorus uptake may be due to the increased volume of soil tapped by the external mycelium. Additional benefits conferred by ectomycorrhizal fungi may include protection against necrotrophic soil-borne pathogens and animals (such as aphids), and increased longevity of the feeder roots. The fungi may provide their hosts with auxins, cytokinins, gibberellins and growth-regulating vitamins. The fungi, on the other hand, are acting as a metabolic sink for the host's carbon. Harley and Smith (1983) stated that the selective advantage of the ectomycorrhizal habit may be the storage of considerable quantities of both soil-derived nutrients and carbon compounds. Mycorrhizae may have the effect of concentrating nutrients in the rooting region, not only by their activities in efficient uptake, translocation and storage during the active stage of their life, but also by later local release as they senesce. Further information on the physiology and ecology of mycorrhizae (including the vesicular–arbuscular mycorrhizae of herbs) are given in reviews by Cooke (1977), Trappe and Fogel (1977), Fogel (1980), Spurr and Barnes (1980) and Harley and Smith (1983). All the results point to the quantitative importance of mycorrhizal fungi (plus any associated fungivorous animals) in nutrient flow between the soil subsystem and the plant subsystem of forests.

Herbs

Net primary production in the herb layer of forests may be high. Hughes (1975) determined net production of above-ground and below-ground parts of the herb flora in a Danish beech (*Fagus sylvatica*) forest with different methods: 74.86 g dry wt m^{-2} yr^{-1} (1340 kJ m^{-2} yr^{-1}) as the difference

between overall maximum and overall minimum biomass; 111.49 g m^{-2} yr^{-1} (1832 kJ m^{-2} yr^{-1}) as the sum of differences between species maximum and minimum; and 160.05 g m^{-2} yr^{-1} (2759 kJ m^{-2} yr^{-1}) as the sum of calculated losses to litter and biomass change. The biomass of this ground flora ranged from 94.57 to 169.43 g m^{-2} (1685–3025 kJ m^{-2}) during the vegetation period from April to November. Maximum biomass for a German beech-wood on limestone was 280 g m^{-2} with *Allium ursinum* as the dominant herb (Eggert, 1985). In a German beech forest on moder soil, maximum herb flora biomass was only 3 g m^{-2} (Ellenberg et al., 1986).

Grazing pressure on the ground vegetation by herbivorous insects or browsing mammals has rarely been quantified. Presumably most of the herb layer net primary production is channelled directly to the detritus food web. Bobek et al. (1979) calculated that roe and red deer consumed 3.2 g dry wt m^{-2} yr^{-1} of herb-layer plants in a Polish deciduous forest, and effected an overall decrease in annual herb biomass production of 9.1 g m^{-2}. Weevil larvae consumed 5.3% of below-ground herb biomass in a Polish oak–hornbeam forest, and 11.6% in a mixed pine (*Pinus sylvestris*) forest (Witkowski and Borusiewicz, 1984). In some cases predation pressure on herbs can be high. The leaf-mining larvae of the syrphid *Cheilosia fasciata* feed on the herb *Allium ursinum*. In a German beech forest, they produced mines that had an area of 44.1% of the total leaf area of the food-plant population (Hövemeyer, 1985).

Litter–soil subsystem: decomposition

The organic remains of plants and animals on the soil surface or in the soil are termed litter. This includes leaves, twigs, fruits, fructescences, bracts, scales of buds, bark flakes and even whole trees, dead roots, carrion and other resource types. Dead materials still attached to the living plants are distinguished from litter as "standing dead" (Satchell, 1974). Comprehensive reviews of plant litter decomposition are given by Dickinson and Pugh (1974) and Swift et al. (1979).

A special, mainly fungal, flora associated with living or senescent plant tissue initiates decomposition before plant litter originates and enters the soil subsystem. On the soil, leaching of low-molecular-weight compounds takes place; this material is fairly rapidly mineralized by bacteria and "sugar fungi". The remaining organic matter is degraded by further saprotrophic organisms — fungi, bacteria and saprophagous animals. Fungi, in particular Basidiomycetes, are generally believed to be most important decomposers of structural plant compounds, such as cellulose and especially lignin. Within ecosystems the decomposition subsystem performs two major functions: the mineralization of essential plant nutrients and the formation of soil organic matter (Swift et al., 1979).

Decomposition as a process

Mechanisms within the process of decomposition are leaching, catabolism, comminution, and humification (Swift et al., 1979) (Fig. 9.2). There are many methodological difficulties in analysing decomposition in deciduous woodland. Major problems emerge from the heterogeneity of the environment, the heterogeneity in the chemical states of the substrates, and the heterogeneity in the types and distribution of decomposer organisms (Parkinson, 1977).

Techniques. Widespread techniques for measuring decomposition rate are estimation of: (1) the weight loss of unconfined litter; (2) weight loss of confined litter ("litter-bag technique"); (3) the disappearance of specific substrates (mostly cellulose); (4) the pathways of isotopes in radioactively-labelled substrates; (5) respiration rates; or (6) enzyme activity (dehydrogenase activity) (Swift et al., 1979).

Many of the methods have drawbacks. This is especially true for the litter-bag technique. John (1980) observed that mesh litter bags restricted access of vegetative fungal structures to confined birch-wood swab sticks, in contrast to unconfined substrates, which showed higher rates of weight loss. Respiration measurements include non-decomposer sources of carbon dioxide, namely root respiration and carbon dioxide production, which originates directly from the consumption of photosynthetic products by mycorrhizal fungi (Harley and Smith, 1983).

Litter input. Leaf material is the main resource category in canopy litter (Table 9.3). Vogt et al. (1986) have given a mean value of "fine above-

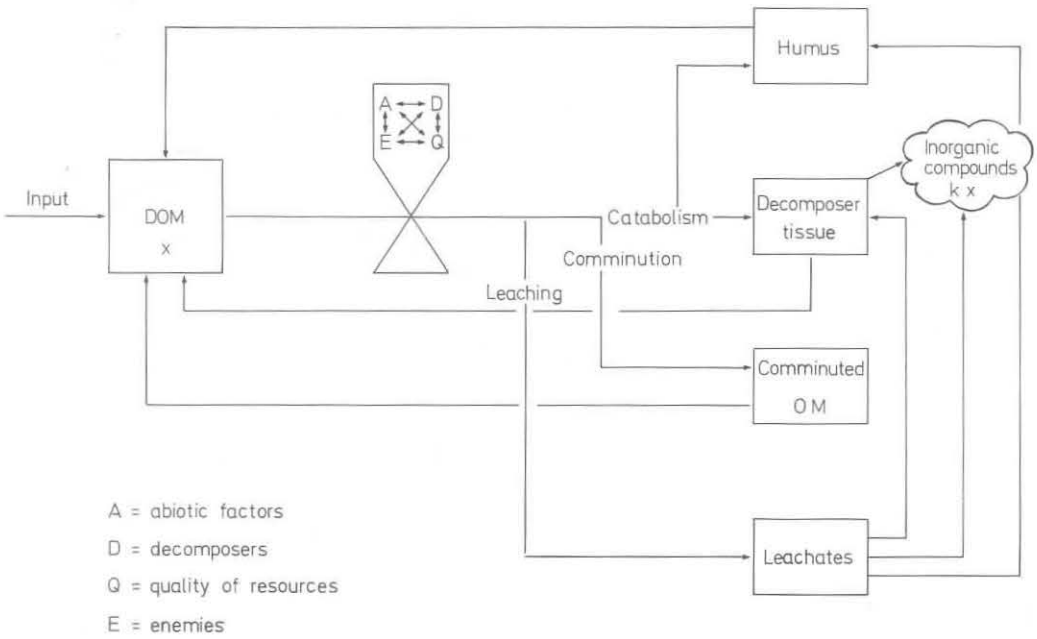

Fig. 9.2. Process of decomposition. k = decomposition rate. Strongly modified after Swift et al. (1979).

ground litter-fall mass" of 385.4 g m^{-2} yr^{-1} for cold temperate broadleaf deciduous forests. Woody above-ground litter-fall with woody input greater than 1 cm in diameter has a mean value of 104.6 g m^{-2} yr^{-1}. Litter-fall decreases with increasing latitude, and is positively correlated with above-ground primary production (O'Neill and DeAngelis, 1981; Vogt et al., 1986). In contrast to grassland ecosystems, part of net primary proportion (NPP) is incorporated into woody material and only a proportion (when dead) is subject to yearly shedding (that is, litter input). The ratio of wood production to litter-fall increases with above-ground net primary production (O'Neill and DeAngelis, 1981). In an English mixed deciduous forest, 66% of NPP enters the decomposer cycle as dead wood and leaf litter (Satchell, 1974). As the distribution of dead wood on the ground is highly clumped, falls of woody litter are underestimated in most studies because of the low number of samples and small collection area (Anderson, 1973a).

On an average, understorey vegetation contributes 9% (range 3–16%), in one case up to 28% of the total litter (Bray and Gorham, 1964), but may reach even higher values. In a Danish beech forest above-ground and below-ground litter-fall in the herb layer was about one-third of above-ground canopy litter-fall (Hughes, 1975).

Below-ground litter input, especially from the death of the abundant fine roots <0.5 cm, is difficult to determine. The contribution of dead roots to total litter input and its significance are just becoming appreciated. In a yellow-poplar (*Liriodeudrou tulipifera*) forest in Tennessee (U.S.A.) estimates of annual root mortality range from 900 g m^{-2} (Harris et al., 1977) to 750 g m^{-2} (Cox et al., 1978). This represents about 75% of the total annual return of organic matter to the soil from both above-ground (litter-fall) and below-ground (root mortality) sources.

Time-course of decomposition. The decomposers normally degrade 40 to 90% of the initial weight of leaf litter input during the first year. Olson (1963) showed a nonlinear rate of weight loss by leaf litter during the first year, with an initial rapid loss of weight, possibly due to leaching of the soluble material. This is followed by a slower rate during the winter months and subsequent acceleration during spring and summer (Swift et al., 1979; Seastedt et al., 1983). Olson (1963) demonstrated that in many cases weight loss is described by the following exponential equation:

TABLE 9.3

Litter input from trees in temperate deciduous forests. Values in g m^{-2} yr^{-1}

Forest(s)	Above-gound litter-fall	Leaves	Wood	Reproductive parts	Bud scales	Below-ground litter-fall	Reference
(A) Single forests							
Beech (*Fagus*) coppice (Blean Woods, England)	467	386	23[d]	17	41		Anderson (1973a)
Chestnut (*Castanea*) coppice (Blean Woods, England)	357	331	26[d]	12	15		Anderson (1973a)
Beech (*Fagus*) forest (Whytham Woods, England)	205–388	151–168[a]	49–58[d]	5–209[b]		92	Phillipson et al. (1975)
Mixed forest (Meathop Wood, England)	542	324	158	60			Satchell from Swift et al. (1979)
Beech forest (Hestehaven, Denmark)	461	279	83[d]	70	29		Nielsen (1977/1978)
Liriodendron forest (Oak Ridge, Tennessee, U.S.A.)	331					750	Cox et al. (1978)
Beech (*Fagus*) forest (Schluttenbach, West Germany)	524 ± 137	395 ± 96	65 ± 28[d]	40 ± 8	25 ± 9		Beck and Mittmann (1982)
Beech (*Fagus*) forest (Göttinger Wald, West Germany)	529	326	108[d]	68	27		H. Kramer and P. Pellinen (pers. comm., 1986)
Beech (*Fagus*) forest (Solling, West Germany)	363–544	257–293	40–145[d]	34–161[c]			Ellenberg et al. (1986)
(B) Comprehensive reviews							
Deciduous forests[e]	320	75%					Bray and Gorham (1964)
Deciduous forests[e] ("Woodland data set")	522 ± 49	85%					O'Neill and DeAngelis (1981)
Deciduous forests	385 ± 21		105 ± 21				Vogt et al. (1986)

[a]Including flowers and bud scales; [b]only fruits; [c]reproductive parts and bud scales; [d]without coarse litter; [e]including other than temperate forests.

$x = x_0 e^{-kt}$

(x, x_0 = resource weights after the time t and at the start of the experiment, k = decomposition rate). According to Wieder and Lang (1982), other exponential models best describe the loss of litter mass over time with biological realism. However, in long-term experiments more organic matter is accumulated than the exponential functions predict (Satchell, 1974), because decomposition rate is slow for some litter components. Presumably the course of decomposition could be best described by summation of the decay curves of the constituents of litter (sugars, cellulose, lignin, etc.) in proportion to the amounts in which they occur (cf. Swift et al., 1979). The sequence of weight loss for litter in a German beech forest on limestone is shown in Fig. 9.3. In the second and following years the decomposition rate decreases, possibly due to higher proportions of more recalcitrant materials. Rate constants (k) for annual leaf-mass loss for six North American deciduous tree species

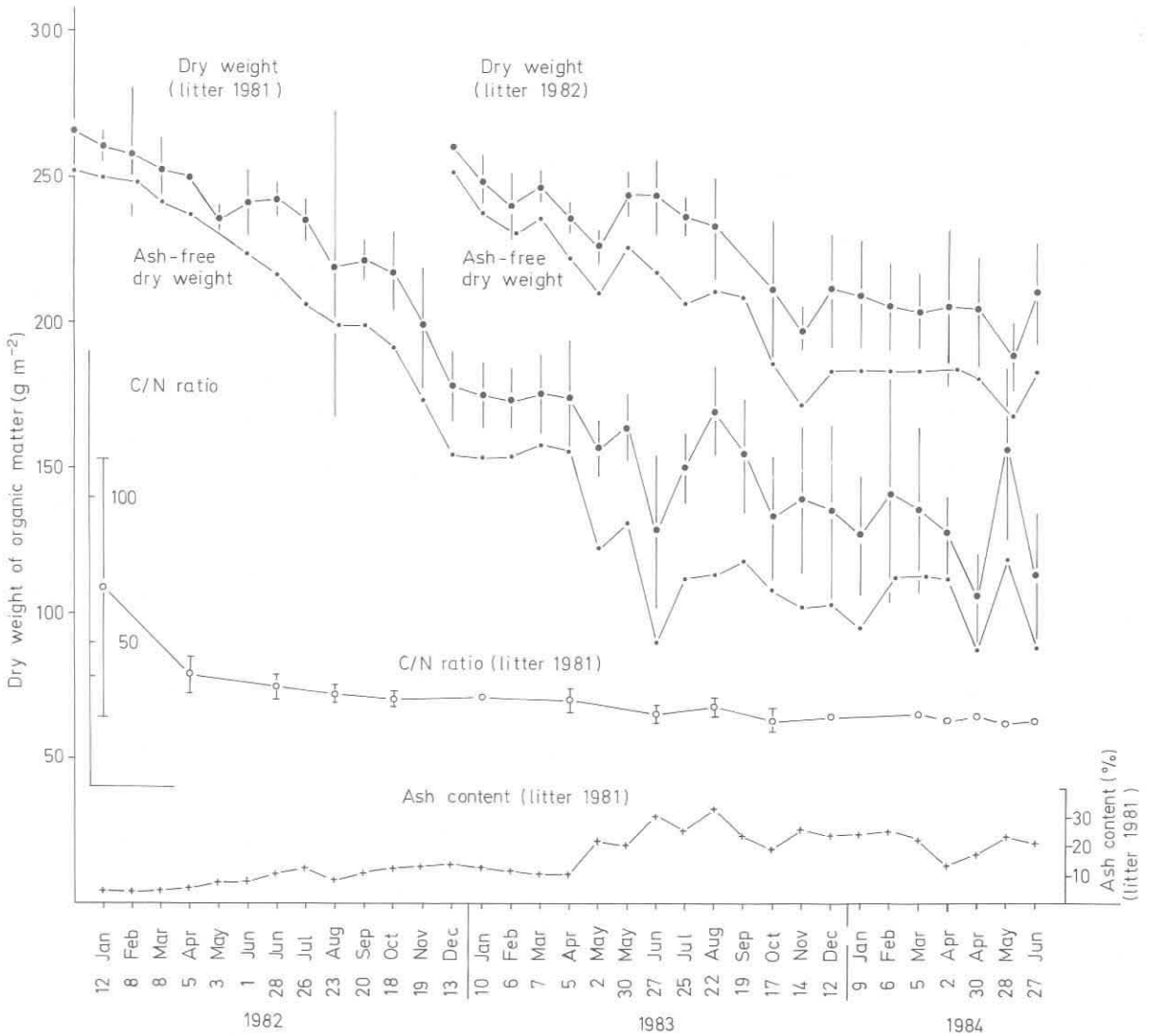

Fig. 9.3. Weight loss of canopy beech leaf litter (mixed with other litter species) in a German beech forest on limestone (Göttinger Wald). The litter material was exposed in containers of 1 m² ground area. The experimental design is described by Schaefer and Schauermann (in prep.).

TABLE 9.4

Nutrient turnover in temperate deciduous forests (data for 14 sites from a review by Cole and Rapp, 1981)

			Organic mass	N	P	K	Ca	Mg
Forest floor organic matter	X	(g m^{-2})	2162.5	37.7	2.5	5.3	20.5	2.8
			150–6635	4.4–105.0	0.2–7.2	0.9–12.3	3.4–51.7	0.5–5.7[a]
Litter-fall	L	(g m^{-2} yr^{-1})	529.9	6.14	0.4	4.16	6.77	1.1
Residence time	X/L	(yr)	4.1	6.1	6.3	1.3	3.0	2.5
Turnover	L/X	(yr^{-1})	0.25	0.16	0.16	0.78	0.33	0.39

[a]Range.

range from 0.08 (*Fagus grandifolia*) to 0.47 (*Fraxinus americana*) (Melillo et al., 1982).

During forest succession the leaf fall and other litter gradually accumulates on the forest floor and decomposition begins. Initially, litter fall may exceed decomposition but eventually an equilibrium is reached between the yearly additions of organic matter and the yearly amount of weight loss due to decomposition. Later, in old, open forests, litter decomposition may exceed litter fall, and the surface layer decreases.

Nutrient release does not necessarily follow the pattern observed for carbon or the whole organic matter on the ground (Table 9.4). Mean residence time is much lower for potassium and phosphorus, is not significantly lower for magnesium, but is higher for nitrogen and calcium.

The constituent processes of decomposition. *Leaching* is a component of weight loss rarely measured in decomposition studies; it may initially occur in the senescent material before litter fall, the leachates reaching the ground via stem flow or drip from the canopy (Swift et al., 1979). Leaching continues in decomposing litter at the soil surface. The leached compounds are mainly utilized by bacteria. *Catabolism* by the biota of litter and soil leads to the evolution of carbon dioxide and the excretion of nitrogenous compounds by animals. *Comminution* by saprophagous animals appears to be an important contribution to decomposition, as the transformation of primary resources to "faecal material" enhances activity of microfloral primary decomposers (see p. 194). *Humification* is a contribution of the fauna and the microflora to soil formation after re-synthesis or direct transformation of food compounds. Humus once formed has a very slow rate of decomposition (Swift et al., 1979).

Influence of driving variables

Decomposition of litter is regulated by a number of variables, including the litter's physical and chemical properties ("resource quality"); climate ("physico-chemical environment"); macro-, meso- and microfaunal responses; and activity of micro-organisms ("composition of the decomposer biota", "influence of enemies") (Swift et al., 1979) (cf. Fig. 9.2).

Though the decay process is very complex, it is probable that the two most important controls of litter decomposition rates are prevailing climatic environment and substrate quality — that is, the susceptibility of the substrate to attack by specialized decomposers (Meentemeyer, 1978). In a review, Edwards et al. (1981) stated that factors which have been shown to affect litter decomposition rates include temperature and moisture (Witkamp, 1966; Reiners, 1968; Meentemeyer, 1978), pH (Katznelson and Stevenson, 1956), substrate quality (Witkamp, 1966; Fogel and Cromack, 1977; Meentemeyer, 1978; McClaugherty et al., 1984) and inhibitors (Macfadyen, 1973). In forest stands at Oak Ridge (oak, pine, maple) in the humid climate of eastern Tennessee (U.S.A.), microbial respiration in litter was controlled in decreasing order by temperature, bacterial density, moisture and the number of weeks since leaf drop (Witkamp, 1966).

Decomposer biota: Microflora. Micro-organisms (bacteria and fungi) are the main agents of decomposition; typically they are responsible for more than 90% of the carbon dioxide, evolved in

forest litter during decomposition (Reichle, 1977; Schaefer, 1989, 1990). This is underscored by high microbial biomass in forest soils (Fig. 9.4).

Fungi are the major group of decomposers (Swift, 1982). For a Danish beech-wood the total amount of mycelium was calculated to be slightly over 100 g dry wt m^{-2}. However, the actual living fungal biomass may be assumed to be only in the order of magnitude of 5 to 10 g m^{-2} (Holm and Jensen, 1980). The biomass value of bacteria was only 1 g dry wt m^{-2} (Holm and Jensen, 1972). In reality this value must be higher, perhaps twice as high (Holm and Jensen, 1980). Kjoller and Struwe (1982) give a range of 63 to 80% of relative fungal respiration in forest soils horizons, obtained with the selective respiration technique. In a British deciduous woodland with mull humus, basidiomycete biomass in the litter layer is about 4.3 g dry wt m^{-2} (Frankland, 1982). A rough estimate for the turnover rate of the mycelium is twenty-two times per year (Swift, 1982), which would correspond with the mobilization of 93% of the available pool of nitrogen and of 110% of the phosphorus during a year. Harley (1971) pointed out the importance of the hyphal structure of the fungi which, in combination with their production of extracelluar enzymes, allows their penetration into substrates such as leaf litter, wood and roots. The "boring" hyphae penetrate intractable portions of the resources, such as the cuticularized surfaces of leaves, seeds and pollen grains (Swift et al., 1979). This mechanical action has been shown to predominate in most cases; however, softening prior to invasion by enzymatic attack on cutin and cell-wall polymers has been proposed in a number of cases. Penetration is followed by a frond-like mycelium which is able to exploit planes of weakness in the substrate (Swift et al., 1979).

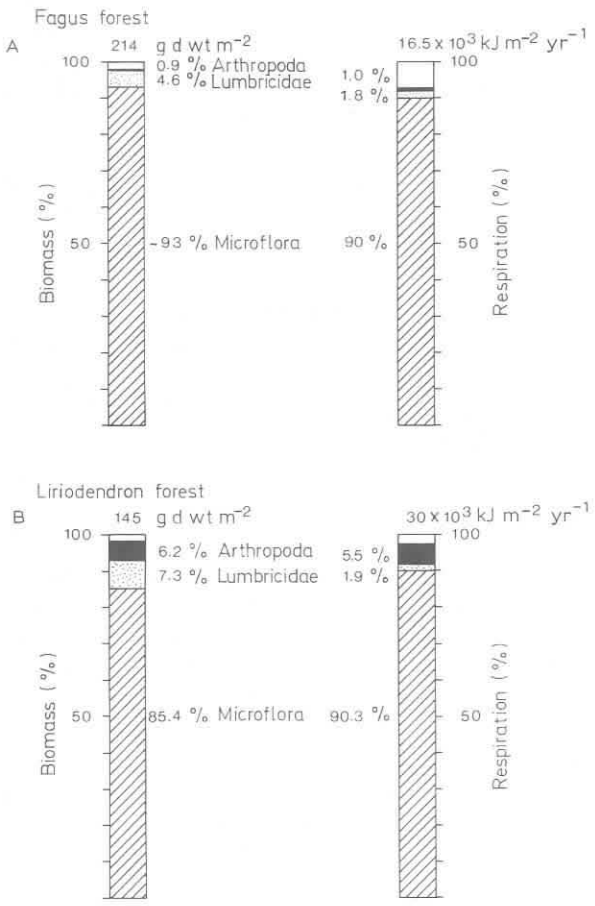

Fig. 9.4. Biomass and respiratory CO_2 evolution for the major groups of decomposer biota in the soil–litter subsystem of temperate deciduous forests. (A) Beech forests on limestone (Göttinger Wald, West Germany) (data from Schaefer, 1982 and 1989b); (B) *Liriodendron* forest (Oak Ridge, Tennessee, U.S.A.) (data from Reichle, 1977; further details in Fig. 9.8).

Decomposer biota: Animals. Saprophagous soil and litter animals directly affect decomposition rates by consuming litter material. However, animals in the soil–litter subsystem have many indirect effects. Anderson and Bignell (1980) suggested that saprophagous invertebrates enhance energy and nutrient flux rates through microbial decomposer populations. Some animal groups in the forest floor act mainly as comminutors (Lofty, 1974). Their feeding activity may increase the surface area of litter material, mobilize materials from resistant tissue, maintain microbial populations in an active growth phase ("grazing", see pp. 87 and 194) and stimulate microbial respiration. Consequently, the study of the composition, population dynamics and activity of soil invertebrates is essential in understanding the dynamics of forest litter decomposition. However, some authors (see, for instance, Smith, 1979) suppose that the fauna is not a rate-limiting factor in decomposition.

Several groups of invertebrates break dead plant material down. Some feed on freshly fallen or decayed litter (primary consumers, "macrohumiphages"), and some are truly detritivorous, feeding on degraded organic matter (secondary consumers,

"microhumiphages"). In many forests earthworms contribute significantly to leaf-litter breakdown by their feeding activities (Anderson, 1973b; Lofty, 1974; Schaefer, 1982). Other primary consumers are diplopods, isopods, dipterous larvae (for instance, Bibionidae: Szabó, 1974; Sciaridae: Hövemeyer, 1985) and oribatid mites (Zinkler, 1971; Wallwork, 1983). Primary decomposers with low assimilation efficiencies and a high rate of comminution, such as isopods, are important in the system.

Data from leaf-litter experiments in mesh bags demonstrate that the larger animals in the litter can consume several times more deciduous (such as oak and beech) leaf tissue (irrespective of age) than can the micro- and mesofauna (Edwards and Heath, 1963, 1975; Edwards et al., 1970). In an early field experiment, Witkamp and Crossley (1966) used litter-bag and gravimetric techniques to measure weight loss and radioactive caesium loss by decaying oak leaf litter. Periodic applications of naphthalene reduced arthropod populations to 20% of controls and increased bacterial populations of the subsoil, but did not generally affect carbon dioxide evolution from litter plus soil. Litter in treated plots retained about 55% of its weight after one year, compared to 40% in control plots. The contribution of microarthropods to decomposition rate of deciduous leaf litter (measured as mass loss in litter bags) ranged from 4% to 49% (Seastedt, 1984). These results are consistent with the hypothesis that the gross effects of soil arthropods include fragmentation of leaf litter.

In the following survey some quantitative data are given on the impact of the fauna on soil biomass and organic matter.

Macrofauna. Earthworms (Lumbricidae) consume a high fraction of the annual leaf-litter fall in a German beech-wood on limestone (Schaefer, 1982) (cf. Table 9.5). In a study by Phillipson et al. (1978), the lumbricids of an English *Fagus sylvatica* woodland respired 215 to 268 kJ m^{-2} yr^{-1}, which is 4.1 to 5.1% of soil respiration. *Lumbricus terrestris* in an English *Fraxinus excelsior–Quercus robur* woodland respired 460 kJ m^{-2} yr^{-1}, which is equivalent to about 5 to 8% of the total soil respiration (Satchell, 1983).

In a German beech-wood, slugs and snails (Gastropoda) consume about 1% of annual above-ground herb and canopy leaf-litter fall (Schaefer, 1982; Corsmann, 1984, and pers. comm., 1986). In an English mixed deciduous forest, snails accounted for 0.54 and 1.23% (according to two independent estimates) of ground litter disappearance (Phillipson and Abel, 1983). The corresponding value for slugs was 1.28 to 1.70% of ground litter disappearance (Phillipson, 1983b). According to a calculation by Mason (1970a), the snails in an English forest ingested 0.35 to 0.43% of the annual litter input. A population of *Arion ater* in an English mixed deciduous woodland ingested approximately 1.54% of the total leaf-litter input (Jennings and Barkham, 1976).

A population of *Trichoniscus pusillus* (Isopoda) ingested about 2.5% of the annual litter input of green phytomass in a German beech-wood (Schaefer, 1982; R. Strüve-Kusenberg, pers. comm., 1986). Stachurski (1974) found that *Ligidium hypnorum* consumed 2% of the annual leaf fall in a Polish alder (*Alnus glutinosa*) forest.

According to Van der Drift (1975), *Glomeris* (Diplopoda) consumed 1.4% of the annual leaf production in a Dutch forest. In a German beech forest this rate amounted to about 2.2% (Schaefer, 1982; T. Sprengel, pers. comm., 1986). Based upon laboratory experiments, Striganova (1974) stated that millipedes are capable of processing 0.5 to 1.2 g of leaves per square metre during the day. According to Ehlert (1980), Isopoda and Diplopoda (Polydesmidae excluded) consumed about 29% of leaf-litter input in a German mixed deciduous forest.

A very rough estimate by Hövemeyer (in Schaefer, 1982) led to the conclusion that larvae of Sciaridae (Diptera) in a German mull forest processed about 8% of the annual input of litter originating from green phytomass. In a German moder forest the Sciaridae and Sciophilidae consumed 13.5 to 29% of the annual leaf-litter fall (Altmüller, 1979).

Meso- and microfauna. At least in some forests, Protozoa are an important group in the carbon metabolism of the soil–litter subsystem. Amoebae consumed an equivalent of about 17% of annual litter fall in a German beech forest on limestone (Meisterfeld, 1986; cf. Table 9.5). Schönborn (1982) calculated a production value of about 50 kJ m^{-2} yr^{-1} for the Testacea in a German mull forest. Total annual ingestion, respiration losses

and egestion losses for testate amoebae in an aspen (*Populus tremuloides*) woodland soil were calculated as 1377, 344 and 826 g wet wt of biomass m^{-2}, respectively. The annual secondary production of Testacea was about 250 to 300 times the standing crop of Testacea in all the soil layers. The dry weight of carbon respired per year by the Testacea was estimated as 16.2 g m^{-2}, which amounted to about 6% of the total carbon input (Lousier and Parkinson, 1984).

In an English mixed forest, Nematoda accounted for 0.13% of total soil respiration ($R = 4.0$ kJ m^{-2} yr^{-1}) (Phillipson et al., 1977). Yeates (1973) found a calorific value of the annual oxygen consumption of 42.3 kJ m^{-2} yr^{-1} for a Danish beech forest, a value that has been corrected to 23.4 kJ m^{-2} yr^{-1} by Yeates (1977). Popovici (1984) determined a respiratory rate of 32.3 kJ m^{-2} over six months in a beech forest of the Western Carpathians. In a German beech forest on mull soil nematodes consumed only an equivalent of 0.2% of annual litter input.

Enchytraeidae contributed to 1.63% of the total soil respiratory metabolism in an English beech forest (Phillipson et al., 1979). For this site the contribution by enchytraeids to soil respiration was about one-third that of earthworms and an order of magnitude greater than that of nematodes. The enchytraeids of a German beech-wood on limestone had a respiration rate of about 170 kJ m^{-2} yr^{-1}, approximately one-half of that of earthworms (cf. Table 9.5; Schaefer, 1990). The enchytraeid worms contributed to about 1% of total respiration of soil biota in this forest.

In a thorough analysis, Luxton (1981) estimated the consumption rate of the oribatid community (Cryptostigmata) in a Danish beech forest as 0.44 to 0.53% of the incoming litter energy, with an annual respiration of 0.11 to 0.13%, much less than that of the mesostigmatid mites in the same forest (Luxton, 1982). For an English forest, Thomas (1979) found a consumption value of 1.1% of litter input. In a German beech forest on limestone, ingestion was only 0.2% on the energy content of litter input. This low energetical significance of forest oribatids is in line with the results of other studies (Petersen and Luxton, 1982; Wallwork, 1983).

For a German beech-wood on limestone, Wolters (1985b) found that Collembola annually consumed about 1.8% of the incoming litter input for green phytomass (cf. Schaefer, 1982), or about 1% of total litter input. Similar low energetical values were obtained for the collembolan community of other forest ecosystems (Petersen and Luxton, 1982).

Effect of animals on the microflora. Soil animals influence the soil microflora by: (1) transmission of microbial inoculum; (2) fragmentation of organic matter; (3) changes in the chemical constitution of organic material during gut passage; and (4) grazing on microfloral population (Szabó, 1974; Parkinson, 1977). Possible effects on the microflora are stimulatory or inhibitory. Only an arbitrary selection of experimental studies on interrelationships between soil fauna and microflora can be given here.

(1) Dissemination of microfloral propagules has rarely been quantified. *Folsomia candida* promotes decomposition in the presence of clay because the collembolans incorporate in the ingesta small amounts of clay, which surround bacterial colonies and are dispersed in the substrate (Touchot et al., 1983). Deposition of glomerid faeces on fresh beech leaf litter increased microbial respiration and the decomposition rate in that organic layer (Sprengel, 1986), obviously by inoculating the leaves with the microflora.

(2) Comminution favours the development of the microflora. Hanlon (1981a) found an inverse relationship between particle size of artificially comminuted oak leaf litter and maximum oxygen consumption levels of bacteria and the fungus *Trametes* (= *Coriolus*) *versicolor* in thin layers. In thicker layers, however, growth of the fungus was reduced, probably as a result of a reduction in pore space.

(3) Microbial growth during passage of food through the gut of *Trachelipus rathkei* is indicated by an increase in bacterial density from leaf to gut to faeces, and by differences in dominant colony types in the gut and faeces compared to food (Reyes and Tiedje, 1976). Gut micro-organisms are dispersed by the isopod, particularly under starvation conditions. Anderson and Bignell (1980) observed that extensive bacterial growth occurs in the pill millipede *Glomeris*. In microcosm experiments, fresh faeces of *Oniscus asellus* and *Glomeris marginata* contained approximately twice the bac-

terial standing crop, but only half the fungal [*Trametes* (= *Coriolus*) *versicolor*] standing crop of mechanically ground oak leaf litter (Hanlon, 1981b). The production of faeces by *G. marginata* led to an increase of microbial respiration for 2 to 3 days. Afterwards microbial activity was lower than on unchanged beech leaf litter (Sprengel, 1986).

Input of faeces from the canopy may accelerate decomposition (Funke, 1973; Satchell, 1974; Nielsen, 1978). According to Zlotin and Khodashova (1980), decomposition of dead plant remains was almost three times faster in the outbreak centres of the oak leaf roller, *Tortrix viridana*, than in non-outbreak areas. Of particular significance is the input of zoogenic material — that is, excrements of leaf insects, their bodies and exuviae and also leaf debris from their feeding, which is high in nitrogen content and other nutrients. Production of excrements by leaf rollers during the period of larval development reached peaks of 60 g dry wt m^{-2}, with an average of 30 g dry wt m^{-2}. The C/N ratio in faeces was 20, in litter 42.

(4) In some cases grazing pressure has been quantified. In a German beech-wood, Protozoa consume 63% of the mean microbial biomass of approximately 240 g m^{-2} (Meisterfeld, 1986). In an aspen (*Populus tremuloides*) site in Canada, the oribatid mites processed about 6 g wet wt m^{-2} yr^{-1} of fungus, which is only 2% of the fungal standing crop (Mitchell and Parkinson, 1976). McBrayer et al. (1974) constructed a model assessing carbon flux in a woodland soil and estimated that all mycophages consumed 86% of the fungal net production. In contrast, Coleman and McGinnis (1970) found that only 0.2% of a laboratory-reared fungus placed in the field was consumed by animals. For a Swedish Scots pine (*Pinus sylvestris*) forest, Persson et al. (1980) estimated that bacterivores and fungivores removed as much as 30 to 60% of the annual production of bacteria in the litter and humus layers. These diverging values demonstrate the uncertainties in estimating the amount of grazing in the soil.

Recent studies have evaluated further the effects of microarthropod grazing on litter-inhabiting fungi and bacteria. Research emphases have moved from considerations of energy flow to those of the possible regulation of nutrient cycling (O'Neill, 1976; Kitchell et al., 1979) and the effects of grazing on microbial activity (Hanlon and Anderson, 1979) and element fluxes (Anderson and Ineson, 1983). Research groups have turned to microcosm studies, which in many cases do not separate effects due to changes in microbial biomass (for instance, by grazing) and the production of faeces, both of which influence the activity of microfloral populations. Hanlon and Anderson (1979) showed that the effects of grazing by *Folsomia candida* on the activity of *Trametes* (= *Coriolus*) *versicolor*, as indicated by oxygen uptake measurements, depended on grazing "pressure". Grazing by five animals per microcosm led to increased respiration, while grazing by higher numbers of animals led to decreased respiration. In cultures containing bacteria and fungi, grazing by *F. candida* caused an increase in bacterial standing crop, but reduced fungal standing crop. Thus high feeding intensities can inhibit microbial activity (Anderson and Ineson, 1983). High grazing intensities by collembolans (*F. candida*) lead to an increase in the leaching of ammonium, nitrate and calcium (Ineson et al., 1982). The inhibitory influence was observed for macroarthropods (*Glomeris, Oniscus*), too, which can effect a reduction in fungal standing crop (Hanlon and Anderson, 1980) and significantly enhance nitrogen mineralization rates through locally reducing fungal immobilization (Anderson and Ineson, 1983). In microcosm studies, collembolans and lumbricids favoured microbial activity in fresh beech leaf litter, whereas diplopods enhanced respiration rates in old litter (Wolters, 1985b; Sprengel, 1986). Visser et al. (1981) used microcosms to assess the effect of grazing by *Onychiurus subtenius* on nutrient release from, and respiration of, a sterile dark fungus. The fungus was very efficient in taking up soluble nitrate and phosphate. Collembolan grazing had no effect in releasing these nutrients during the ten-day experiment. Significant increase in respiration of litter colonized by the fungus was observed following collembolan grazing, but this increase was attributed to the activity of bacteria and fungi, "contaminants" brought into the leaf litter system by the Collembola. Thus the use of non-sterile animals has indicated the important effects of "tracked-in" micro-organisms (particularly bacteria) in nutrient dynamics and litter respiration effects, which can override specific grazing effects of the mesofauna.

Microcosm experiments with nematodes and bacteria demonstrated that the presence of nematodes leads to higher nitrogen mineralization rates (R.V. Anderson et al., 1983).

There are only a few studies on the actual amount of element mobilization in the forest floor effected by animal populations. The additional nitrogen mineralization caused by a population of *Aporrectodea caliginosa* in a beech-wood on limestone was calculated to be 0.42 g N m^{-2} yr^{-1} (Scheu, 1987). Anderson and Ineson (1984) evaluated the importance of animal–microbial interactions in nutrient-flux pathways of forest ecosystems. The feeding activities of animals enhance nitrogen mineralization by micro-organisms and change the temporal pattern of nitrogen mineralization in the surface litter layers so that nitrogen is released into solution even at high C/N ratios and reaches the sub-horizons where it can be utilized by ectotrophic mycorrhizae.

However, Seastedt (1984) reviewed the effect of microarthropods on nutrient dynamics in the soil, and reported that increased mineralization of nitrogen, phosphorus, and potassium is observed in only a part of the studies. Stimulation of microbial activity by animals may result in immobilization of these elements by incorporation into microbial tissue.

Resource quality: general aspects. Rate of litter decomposition depends on "resource quality characteristics", among others C/N ratio, lignin content, and the concentration of secondary plant substances (Bosatta and Staaf, 1982; Mellilo et al., 1982).

Generally, herb litter is more readily decomposed than canopy leaf litter (Heath et al., 1966), probably because of lower C/N ratios, lower cellulose and lignin content and lower "toughness" of herbs.

Secondary compounds can modify the rate of decomposition. For instance, a study by Summers and Lussenhop (1976) revealed that juglone under walnut (*Juglans regia*) trees causes a decrease of soil arthropod density and an accumulation of soil organic matter under the canopy.

Special resource types are carrion (studied for instance by Putman, 1978), arthropod remains (Seastedt and Tate, 1981), macrofungi and hyphal structures (Parkinson, 1977), dung (Lodha, 1974), invertebrate faeces (Nicholson et al., 1966; Hanlon, 1981b) or pure substrates in experimental studies, such as cellulose (Parkinson, 1977).

Decomposition of roots has been rarely studied (see, for instance, Parkinson, 1977; Cox et al., 1978). The sloughing-off of dead tissue and the production of root exudates during root growth increase the amount of soil organic matter, but rates of input are difficult to quantify. Little information exists on the rates of decomposition of dead roots (Parkinson, 1977). The rhizosphere and attendant root regions (for instance, root surface microflora, mycorrhizae) have been intensely studied, but the relation of these phenomena to decomposition is not known. In a North American mixed deciduous forest in Virginia, fine roots (less than 3 mm in diameter) decomposed slowly; after four years roots had lost between 20 and 60% of their initial mass (McClaugherty et al., 1984). Fine roots accounted for at least 25% of soil organic matter in the hardwood.

Resource quality: leaf litter from the canopy. Litter species may have different rates of decomposition. In a Belgian oak forest on calcareous soil, Mommaerts-Billiet (1971) observed low loss rates for *Fagus sylvatica* and *Quercus robur* and high loss rates for *Acer pseudo-platanus*, *Carpinus betulus*, *Prunus avium*, *Tilia platyphyllos* (cf. Swift et al., 1979). In a German beech forest on limestone, weight loss of litter decreased in the sequence *Fraxinus excelsior*, *Acer* spp., *Fagus sylvatica* (see Chapter 6, Schaefer, personal observation). Shade leaves of beech were more readily decomposed than sun leaves. Similarly, Heath and Arnold (1966) observed that shade leaves of oak (*Quercus robur*) and beech disappeared faster than sun leaves.

Fresh leaf material may remain unpalatable to soil fauna until the polyphenols are removed (Edwards and Heath, 1963; Satchell and Lowe, 1967), which may delay faunal attack on the litter for some time (Gist and Crossley, 1975b). Fogel and Cromack (1977) found decomposition rates of leaf litter to be more closely related with lignin content than with C/N ratio. However, soil animals fed on chestnut (*Castanea sativa*) leaf litter to a far greater extent than beech (*Fagus sylvatica*) leaves, although chestnut leaves contained higher polyphenol concentrations than beech leaves

(Anderson, 1973c). Additionally, these differences were not directly attributable to differences between the nitrogen contents or C/N ratios of the two litter species.

According to Kovács (1977), decomposition of green leaves of *Acer tataricum*, *Cornus mas*, *Quercus cerris* and *Q. petraea* was more rapid than decomposition of fallen dry leaves. Presumably the high nitrogen content of the green leaves is the cause. More than 50% of the biogenic elements were released in the first 4 to 5 months. Leaves of some bushes yielded more nutrients than the leaves of *Quercus*.

Edwards and Heath (1975) made studies with mesh bags containing oak and beech leaves collected from June to October (and in the litter from November to December). As the leaves on a tree become older they gradually become less palatable to soil animals, just as they do to those arthropods that feed on them whilst they are still on the tree. There seems to be one basic difference between the aging of oak and beech leaves. Whereas beech becomes progressively less palatable throughout the growing season and continues to be so even after several weeks in the leaf litter, oak, although it becomes less palatable whilst on the tree, is much more palatable to the soil animals once it is in the litter and has lost polyphenolic material through weathering.

Resource quality: dead wood. Although branch-wood and trees may form a large part of the litter-fall in temperate forests (see p. 187), yet this type of litter has been largely ignored in decomposition studies in comparison with leaves (Swift et al., 1976). In the canopy, dead wood can be present as dead trees and as dead branches on trees that are still living. The pool of attached and standing dead wood amounted to 4.3% of total above-ground woody biomass in a Danish oak (*Quercus robur*) forest (Christensen, 1977). In an English mixed forest the dead-tree standing crop was equivalent to about 14% of total dead wood in the canopy (Swift et al., 1976). Swift et al. (1984) estimated dead wood on the forest floor to be 311 g m^{-2} on one site and 311 to 440 g m^{-2} on another site in an English coppiced beech–oak woodland. These authors review other studies on deciduous woodlands and give a range for dead wood on the forest floor between 228 and 914 g m^{-2}. These values are of the same magnitude as leaf-litter standing crops. Relative density (g dry wt cm^{-3}) is widely used as a measure for the extent of decay of woody litter (Swift et al., 1976; Christensen, 1984). As a study of the decomposition of branch-wood greater than 2 cm in diameter revealed, leaching, microbial catabolism, animal consumption and export contribute to the decay process (Swift et al., 1976). Three phases of decomposition were observed. After dying, branches in the canopy were colonized by fungi and decomposed at an annual loss rate of about 8.4% (Fig. 9.5). At branch-fall the wood had lost about 40% of its original weight. On the forest floor the average annual rate of weight loss due to decomposition was 17.1%. In the first phase fungi were predominant, but wood-boring insects invaded shortly after branch-fall. Decomposition rates did not differ significantly between branches of four species of trees (*Betula* spp., *Corylus avellana*, *Fraxinus* and *Quercus* spp.). For a Danish oak (*Quercus robur*) wood, Christensen (1984) showed that the mean weight loss of attached wood was 18%, the weight loss of dead wood on the soil surface 43%. All these studies demonstrate a considerable weight loss prior to litter-fall. Decay rates of woody litter on the ground are lower than those for leaf litter. For the chestnut oak, *Quercus prinus*, in a North American hardwood forest, Seastedt and Crossley (1981) observed that twigs and branches lost mass at rates 40% of those for leaf litter. In a Danish oak forest, the decay

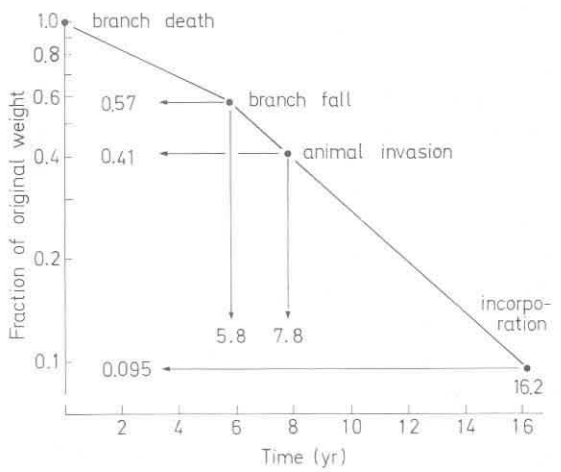

Fig. 9.5. Decomposition of branch-wood greater than 2 cm in diameter in an English mixed deciduous woodland (Meathop Wood). Modified from Swift et al. (1976).

constant for dead oak wood on the soil surface was $k = 0.26\ yr^{-1}$, for total soil dead wood (soil surface dead wood litter and disintegrated dead wood and humus fraction of dead wood) $k = 0.034\ yr^{-1}$ (Christensen, 1977).

Wood-inhabiting invertebrates regulate wood decomposition processes by four mechanisms (Ausmus, 1977): nutrient input by defaecation; inoculation of the wood with microbial spores and cells; grazing on microbial populations, thus influencing succession, catabolism and nitrogen fixation rates of the microflora; and creation of spatial heterogeneity within woody substrates. Ants may interfere with wood decomposition. In a Russian oak forest, *Formica polyctena* concentrated 17.5% of annual branch-fall in its nests, which covered only 0.8% of the forest floor. The ants created "high nutrient content points" (Pokarzhevskij, 1981).

Generally on the floor of temperate deciduous forests logs (> 7.5 cm in diameter) have a larger mass per square metre than branches (2 to 7.5 cm) (Triska and Cromack, 1979). 42.5% of the soil-surface dead wood in a Danish oak forest consisted of components with a diameter ≤ 2 cm (Christensen, 1977). Finely divided wood debris is more susceptible to microbial and animal attack than large woody debris with its low surface-to-volume ratio. The latter requires hundreds of years to decompose (Triska and Cromack, 1979). In a North American hardwood catchment, woody litter of *Quercus prinus* had an annual decay coefficient k of 0.1524 for diameter class 0 to 1 cm, 0.1728 for 1 to 3 cm and 0.0912 for 3 to 5 cm (Abbott and Crossley, 1982). Harmon et al. (1986) cited decay rates k for log–bole mineralization between $k = 0.52\ yr^{-1}$ (*Liriodendron tulipifera*) and $k = 0.029\ yr^{-1}$ (*Quercus* spp.). Wood decay occurs both from the outside inward and from the centre to the outside. Moisture content of decomposing coarse debris increases with age and facilitates decomposition by preventing drying out during summer. As log decay advances, there is a progressive increase in the concentration of essential nutrients such as nitrogen and phosphorus, and a progressive decrease in density. One of the major obstacles to the decomposition of wood debris is its extremely high carbon/nitrogen ratio (Triska and Cromack, 1979). Another problem is the biodegradation of lignin.

Mechanisms of lignin biodegradation are still largely matters for speculation (Crawford, 1981); however, it is obvious, based on what is known of lignin structure, that these biodegradative mechanisms must be unusual and perhaps unique. Primary decomposers attacking lignin or lignocellulose are fungi (white-rot, brown-rot and perhaps soft-rot fungi) and bacteria (Crawford, 1981). White-rot basidiomycetes appear to be most important (Swift, 1977; Levy, 1982; Mercer, 1982), although lignins are not readily utilizable as a carbon/energy source by these fungi. Evidence thus far strongly indicates that white-rot fungi probably do not significantly degrade natural lignins in the absence of an additional, more readily metabolized, carbon source.

Lignin and other polyphenolic substances have been considered a possible sink for nitrogen in litter (Berg and Staaf, 1981). Field studies have revealed that lignin concentration influences the nitrogen immobilization capacity of various litter types. To some extent such an influence might be indirect, acting through its effect on microbial activity (Bosatta and Staaf, 1982). Recently Aber and Melillo (1982) found evidence of an influence of the lignin level *per se*, a higher initial lignin concentration in forest litter giving a stronger immobilization capacity. The authors argued that a high lignin level would tend to reduce microbial utilization rates by producing prehumic substances with the ability to incorporate nitrogen.

Physico-chemical environment. Temperature and soil moisture are the most important abiotic factors influencing the rate of decomposition. Some types of litter are primarily comminuted by abiotic processes such as wind, rain, hygroscopic movements — for instance *Castanea* leaf litter (Anderson, 1973b).

The effect of temperature is underscored by the fact that decomposition rates usually are higher in the warmer seasons of the year. Of the variability in carbon dioxide evolution rates observed on a *Liriodendron* forest floor, 94% was accounted for by the litter temperature squared (Edwards et al., 1981).

According to Meentemeyer (1978), moisture controls rates of decomposition. Moisture has a pronounced effect, especially in drier forest ecosystems. Reiners (1968) and Froment (1972) reported

direct correlations between soil moisture and soil respiration in oak forests, while DeSanto et al. (1976) found an inverse correlation between carbon dioxide evolution rates and soil moisture in a beech (*Fagus sylvatica*) forest in Italy. In the latter forest, soil moisture was rarely lower than 70% of the soil dry weight. In a *Liriodendron* forest there were no statistical correlations between forest floor respiration and moisture, where moisture was seldom limiting. Meentemeyer (1978) has suggested that actual evapotranspiration can be used to predict decomposition rate.

The forest floor topography may cause different microclimatological conditions. In a Canadian beech (*Fagus grandifolia*)–maple (*Acer saccharum*) forest consisting of high sites and low sites (with a 0.5 m maximum difference in elevation), average litter accumulation (April to October) was 416.2 g dry wt m^{-2} and 2438.3 g dry wt m^{-2} on high and low sites respectively because of the action of the wind (Dwyer and Merriam, 1981). At the low sites, temperature variability of the litter–soil interface was reduced to 13% of the mean by the presence of the thick surface litter layer and by the greater heat capacity of moist litter. Average bacterial populations were approximately 3.5 times larger in low sites. Here the diversity of litter types and ages was high, decay rates were enhanced, and the soil was characterized by greater incorporation of organic fragments and humus formation.

The influence of abiotic factors may vary seasonally and in a diurnal rhythm. In a mixed oak (*Quercus robur*) forest in Belgium during the leafless phenological phase, a positive correlation was found between the rate of carbon dioxide production and the mean soil temperature at both 1 cm and 10 cm depth. During the leaf phenological phase, a positive correlation existed between the rate of carbon dioxide production and the water content of soil (Froment, 1972). As McBrayer and Cromack (1980) showed for a North American oak forest, decomposition continues throughout the winter under the snow cover, but may cease periodically when litter and soil temperatures fall below about 0 °C. According to Edwards and Sollins (1973), in a deciduous forest carbon dioxide evolution increased at night, especially during dry periods. Here the moisture and the temperature of the air may be important variables determining the rate of movement of carbon dioxide from the forest floor into the atmosphere. Since dew formation on the dry litter may enhance microbial metabolism, it is noteworthy that the night-time peak in the carbon dioxide curve is due mainly to increased carbon dioxide evolution from litter and not from soil.

"Predation". Predation pressure by arthropods of the litter and soil layers is high. However, the influence of predators on decomposition rate has rarely been studied experimentally. After elimination of predators by an insecticide (mirex), the consumption rates of saprophagous animals increased (Crossley, 1977). A similar effect was observed for other soil and litter animal communities. For instance, Clarke and Grant (1968) recorded higher densities of saprophages after experimentally removing spiders as predators in the litter layer.

Special predator–prey relationships between soil fauna groups have been found. Two examples are Chilopoda–earthworms (T. Poser, pers. comm., 1986) in a German beech forest, and *Rhodacarus* sp. gr. *roseus–Folsomia penicula* in a French oakwood (Cancela de Fonseca et al., 1979). The existence of these trophic links may lead to the conclusion that the consumption rates of populations of saprophages and microphytophages are reduced by predation pressure. This, however, is difficult to quantify.

Decomposition in mull and mor soils

Decomposition rates are generally higher in mull than in moder or mor forest soils (Herlitzius and Herlitzius, 1977; Swift et al., 1979; Herlitzius, 1983), contributing to a lower standing crop of soil organic matter in the first soil type (see Chapter 14). The reason for the different decay rates in these soil types are complex. Higher rates in mull soils are the result of litter comminution by the macrofauna, mixing of organic material with the mineral soil and the maintenance of well-drained aerobic conditions in the soil. Mor soil, on the other hand, has low pH values in all strata (produced by acid litter or acid soil parent material), which inhibit the macrofauna and prevent its feeding and burrowing activities (Swift et al., 1979). Additionally, decomposition may be inhibited in moder and mor soil by the presence of phenolic acids in litter and by the water-holding

capacity of organic material (Dickinson and Pugh, 1974; Swift et al., 1979).

ENERGY FLOW IN THE WHOLE ECOSYSTEM

Energy flow can be described in units of energy, of biomass or necromass, and as carbon flow.

The tentative energy budget for a deciduous woodland by Satchell (1971) on an I.B.P. site is perhaps the first analysis of such a kind in which the biomass of different components of the soil and litter biota are given (Parkinson, 1977). An earlier attempt to quantify energy flow in forests was made by Varley (1970). Recent syntheses of carbon metabolism in temperate deciduous forests have been provided by Spurr and Barnes (1980), Edwards et al. (1981) and Grimm and Funke (1986).

In order to compare energy flow in different forest ecosystems and to draw general conclusions, a German beech (*Fagus sylvatica*) forest on limestone with mull soil (Göttinger Wald), a German beech forest on moder soil (Solling) and a North American yellow poplar (*Liriodendron tulipifera*) forest (Oak Ridge) are analyzed in more detail. The animal component in these study sites is comparatively well known.

Well-studied ecosystems

Beech forest (Göttinger Wald)

A survey of the energetics of the animal groups in the beech forest Göttinger Wald has been given by Schaefer (1982, 1989). The present knowledge, with some preliminary data, is summarized in Table 9.5. (A recent synthesis is given by Schaefer, 1990.) Rhizopods, enchytraeids and especially earthworms are the energetically most significant groups of soil fauna.

From a preliminary energy budget (Fig. 9.6) some general principles emerge.

(1) Consumption (C) of living plant material is remarkably low. The value $C = 65$ kJ m^{-2} yr^{-1} includes only curculionid and lepidopteran populations. Feeding pressure by non-phyllophagous canopy arthropods, by herbivores in the herb layer, by browsing mammals and by rhizophages is not known. According to a special study (Hövemeyer, pers. commun., 1986) the larval population of the leaf-mining syrphid *Cheilosia fasciata* consumed 263 kJ m^{-2} yr^{-1} in pure stands of the herb *Allium ursinum*. Presumably total consumption of plant material by phytophages does not exceed a value of about 1% of NPP.

(2) Total consumption of dead organic matter and/or microbial biomass by "saprophages" (including microphytophages) is of the same order as the amount of total annual leaf litter-fall. However, the value of litter input does not include larger woody debris, and contains a conservative estimate of below-ground litter production by trees. Most of the material consumed is recycled to the compartment "dead organic matter" via egestion *FU*. Total animal metabolic activity in the soil–litter subsystem (about 10% of respiration of soil biota) is low compared to microfloral metabolism (about 90% of respiration of soil biota). The latter value was determined indirectly by subtracting animal respiration from energy content of litter input. An independent estimate of soil respiration was given by Andres (1984). He measured an annual output of 273 g C m^{-2} yr^{-1} by animals and microflora (after subtraction of root respiration) on plots without herbs, corresponding to a value of about 12 000 kJ m^{-2} yr^{-1}. K.H. Domsch and M. Vanselow (pers. comm., 1986) calculated an output of carbon of 370 g C (16 500 kJ) m^{-2} yr^{-1} by microflora populations.

(3) Consumption rates by zoophagous predators (parasitoids are not included) correspond in order of magnitude to production rates of all forest animals. Hence overall predation pressure appears to be high in this forest ecosystem.

Beech forest (Solling)

Similar regularities emerge for this forest on moder soil (Fig. 9.7) (Grimm and Funke, 1986). Presumably consumption rates by "saprophages" are lower than in the beech mull soil, because mean annual biomass of all saprophages is only 5 to 6 g m^{-2} in the Solling forest (Schauermann, 1986). Consequently, microfloral respiratory metabolism appears to be even more important in this ecosystem. Catabolism of the microflora is reinforced by the high proportion of microphytophagous animals grazing on the microflora (cf. table in Schauermann, 1986).

TABLE 9.5

Energy budget for the animal groups in a beech-wood on limestone (Göttinger Wald)

Animal group[a]	Trophic type[b]	Mean annual biomass (B) (g m^{-2})	Respiration (R) (kJ m^{-2} yr^{-1})	Production (P) (kJ m^{-2} yr^{-1})	Assimilation (A) ($R+P$) (kJ m^{-2} yr^{-1})	Consumption (C) (kJ m^{-2} yr^{-1})	Egestion (FU) ($C-A$) (kJ m^{-2} yr^{-1})
Flagellata	mi/sa	0.054	26	20	46	100	54
Rhizopoda	mi/sa	1.476	764	588	1352	2938	1586
Turbellaria	zo	0.008	4	2	6	12	6
Nematoda	zo/mi/sa	0.024	73	11	84	167	83
Rotatoria	sa/mi	0.005	5	1	6	11	5
Gastropoda	sa/ph	0.430	29	29	58	83	25
Enchytraeidae	sa/mi	0.600	177	70	247	1077	830
Lumbricidae	sa	10.700	298	141	439	8788	8349
Tardigrada	zo/mi/sa	0.004	3	1	4	7	3
Araneida	zo	0.135	5	2	7	7.5	0.5
Pseudoscorpionida	zo	0.016	0.7	0.9	1.6	2	0.4
Opilionida	zo	0.011	0.5	0.7	1.2	1.5	0.3
Gamasina	zo	0.045	5	2	7	9	2
Uropodina	mi	0.026	1.5	1	2.5	9	6.5
Cryptostigmata	mi/sa	0.180	7	7	14	31	17
Harpacticoida	mi/sa	0.002	1.4	0.9	2.3	7.7	5.4
Isopoda	sa	0.093	41	13	54	208	154
Diplopoda	sa	0.618	12	24	36	182	146
Chilopoda	zo	0.265	33	14	47	58	11
Collembola	mi/sa	0.153	23	15	38	152	114
Carabidae	zo	0.144	4	6	10	12	2
Staphylinidae	zo	0.076	12	16	28	35	7
Curculionidae[c]	ph	0.064	5.9	2.4[f]	14.7	58.7	44
Lepidoptera	ph		5.3	0.8[f]	13.3	55.5	42.2
Diptera, larvae	sa[d]	0.119[e]	5[d]	3[d]	8[d]	669[d]	651[d]
Phytophages			11.2	3.2[b]	28	114.2	86.2
Saprophages/Microphytophages			1367.9	919.7	2346.6	14 342.7	11 996.1
Zoophages			102.2	48.8	151.0	224.0	73.0

[a]Some, mostly minor, groups are omitted (Ciliata, Acarina except Cryptostigmata and Mesostigmata, Symphyla, Diplura, Protura, Orthopteroidea, Psocoptera, Thysanoptera, Rhynchota, Neuropteroidea, Hymenoptera, many Coleoptera). Data combined from many authors (cf. Schaefer, 1982; Meisterfeld, 1986; see Chapter 14). Some values are preliminary. A recent synthesis is given by Schaefer (1990).

[b]mi: microphytophagous; ph: phytophagous; sa: saprophagous; zo: zoophagous. Half of the biomass of Nematoda and Tardigrada is regarded as zoophagous, half of the biomass as saprophagous and/or microphytophagous.

[c]Any other canopy Coleoptera.

[d]Only Sciaridae.

[e]All dipterous larvae.

[f]Production of adults.

Liriodendron forest (Oak Ridge)

Grazing pressure by phytophages is also low in this forest, pressure by predators is high and microfloral contribution to carbon metabolism far more significant than that by animals (Fig. 9.8) (Harris et al., 1975; Reichle, 1977; Edwards et al., 1981). Harris et al. (1975) reported an annual average for the standing carbon pool of 58 g m^{-2} in the forest-floor microflora as compared to about 7 g C m^{-2} in invertebrates. Phytophages include only canopy arthropods, and the microfauna is omitted in the compartment "saprophages" [see detailed table in Reichle (1977) presenting the taxa studied].

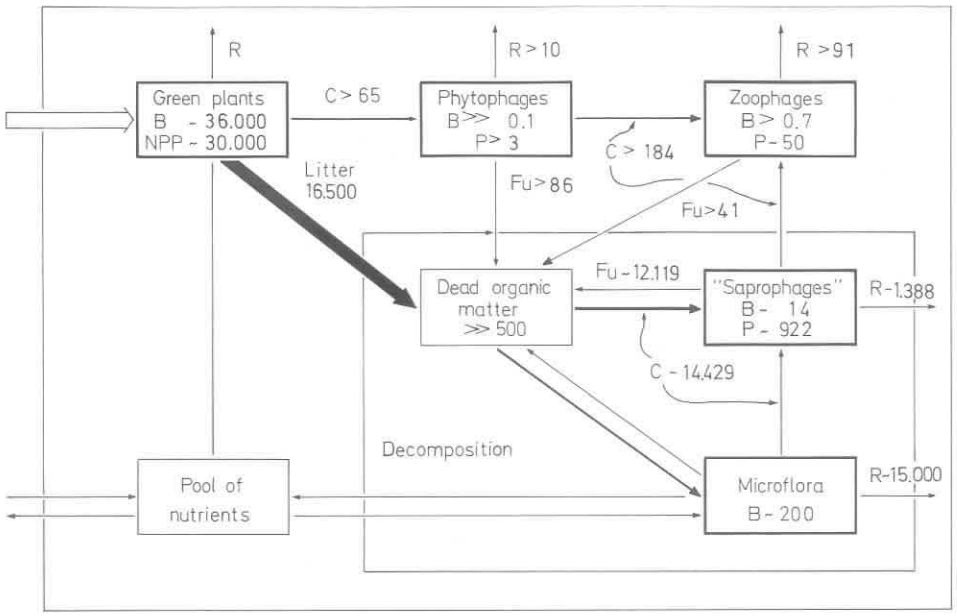

Fig. 9.6. Energy budget of the fauna in a beech-wood on limestone (Göttinger Wald). Values for animals are taken from Table 9.5. B=mean annual biomass in g dry wt m^{-2} (about 21 kJ for plant mass, about 17 kJ for animal mass); R=respiration, P=production, A=assimilation, C=consumption, FU= egestion (all values in kJ m^2 yr^{-1}). Litter data from H. Kramer and P. Pellinen (pers. comm., 1986), not including larger wood debris; root litter production estimated as 25% of above-ground litter input; estimate for herb litter by Eggert (1985). Biomass of microflora after K.H. Domsch and M. Vanselow (pers. comm., 1986). B of dead organic matter refers only to litter on topsoil. A more complete, updated budget is given by Schaefer (1990).

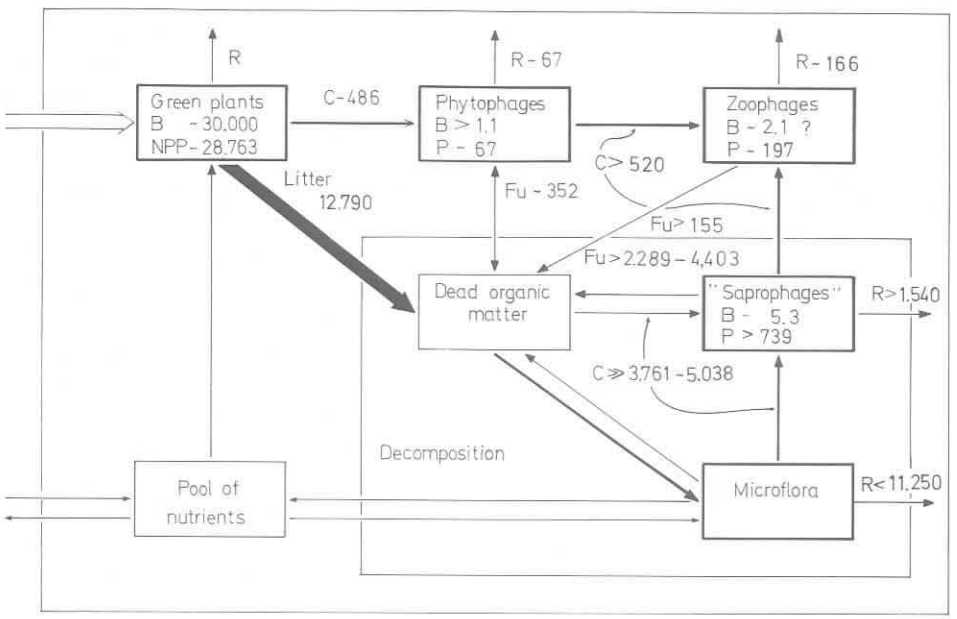

Fig. 9.7. Energy budget of the fauna in a beech-wood on moder soil (Solling). Values from Grimm (1977), Ellenberg et al. (1986), Grimm and Funke (1986) and Schauermann (1986). Data for Testacea not included. Abbreviations in Fig. 9.6.

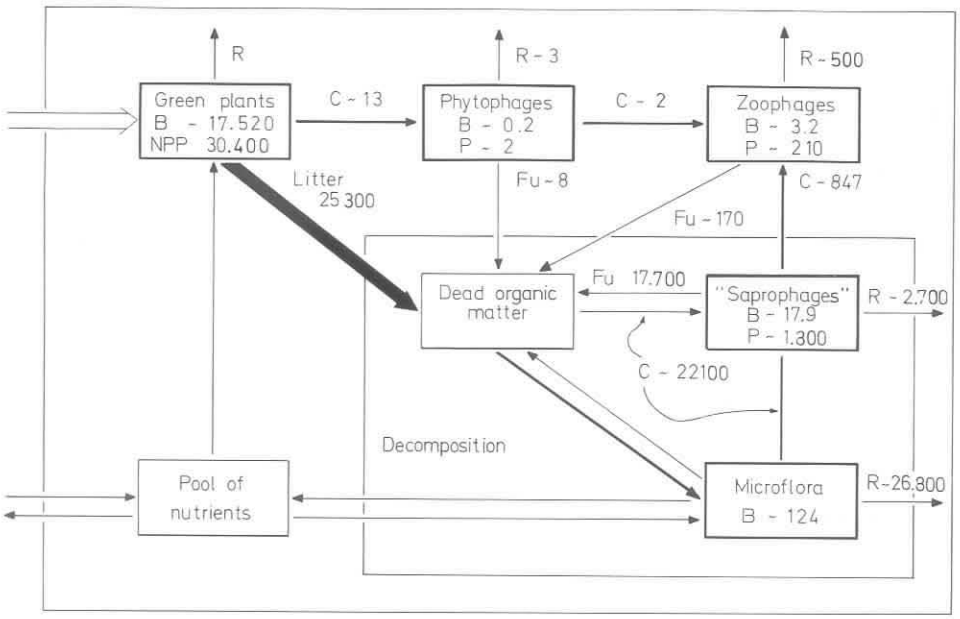

Fig. 9.8. Energy budget of the fauna in a *Liriodendron* forest (Oak Ridge). Combined after Harris et al. (1975), Reichle (1977) and Edwards et al. (1981). The numbers for g carbon were transformed to energy values by using the equations 1 g C = 22.4/12 l CO_2; 1 l CO_2 = 23.9 kJ (cf. Petrusewicz and Macfadyen, 1970). Abbreviations in Fig. 9.6. Calculating C and P from the data for annual respiration (in Reichle, 1977), the following ecological efficiencies were used: $P/A = 0.4$ (phytophages, saprophages), 0.3 (zoophages); $A/C = 0.4$ (phytophages), 0.2 (saprophages), 0.8 (zoophages).

Synthesis

Only about 1% (0.01–3.5%: Whittaker, 1975) of the energy of solar radiation is fixed by plants as gross primary production (GPP). Part of GPP is respired by the plants, and part of it is channelled to net primary production (NPP) (34% in a *Liriodendron* forest (Oak Ridge); 57% in a Danish beech forest (Hestehave); 39% in a British oak forest; 62% in a Polish oak–hornbeam forest: see Edwards et al., 1981). NPP is composed of annual growth, and equals the sum of the biomass increment dB_A, litter fall L_A and consumption by herbivores C_H ($NPP = dB_A + L_A + C_H$) (Runge, 1973). Leaf biomass is only a small fraction of branch and bole biomass: 2.2% for temperate broadleaved deciduous forests, according to the woodland data set (Burgess, 1981). However, leaf material of trees is about one-third of NPP. Total zoomass is low and is mainly a part of the soil–litter subsystem; it is only a fraction (about 5–20%) of microbial biomass.

Herbivore food web

According to Whittaker (1975), the average herbivore consumption is less than 0.2% of NPP in temperate deciduous forests. Runge (1973) gives a value of 1.0 to 2.5% of NPP. Satchell (1974) estimated herbivore consumption to be only 0.1% of NPP in an English deciduous forest. Annual consumption of photosynthetic material is 5 to 10% of NPP (Springett, 1978). These consumption rates are lower than those for temperate grasslands (Petrusewicz and Grodzinski, 1975; Whittaker, 1975).

A better measure of the impact of herbivores on phytomass is MR (= material removed), which is related to consumption C by the equation $C/MR = 0.8$ (Grimm and Funke, 1986). However, even when MR is taken into account, the removal of plant material remains low. It should be emphasized that only a part of NPP is available as food. Although this value is difficult to quantify, it is suggested that the amount of available food is lower in forests than in herbaceous ecosystems, in which the grazing food web is considerably more important (Whittaker, 1975). For instance, for forest rodents only 4.5% of the total NPP may be regarded as available food (Petrusewicz and Grodzinski, 1975). However, in many forested ecosystems energy utilization by rodents is usually less

than 0.5% (Ryszkowski, 1969; Grodzinski et al., 1970). Golley et al. (1975) have given consumption values between 0.6 and 4.6% of NPP available for small mammals. Presumably only a small fraction of available food is utilized by herbivorous forest vertebrates and invertebrates.

Saprovore food web

Most of annual NPP is transformed to litter (57.5% of above-ground NPP, according to the woodland data set: Burgess, 1981). More than 50% of the carbon in a forest ecosystem occurs as dead organic matter (detritus) on the ground surface or incorporated into the soil (Edwards et al., 1981). Additionally, a large flux of organic matter below-ground is a general property of forest ecosystems; it is a seasonal phenomenon leading to prompt metabolism of part of the root detritus by the soil biota (Ulrich et al., 1981).

Total consumption of dead organic material (and microbial biomass) by litter- and soil-dwelling "saprophages" (including microphytophages) appears to approximate the amount of annual litterfall (see Figs. 9.6–9.8). In further studies the following annual consumption rates are cited: about 40% (Sukachev and Dylis, 1964), 33% (Edwards, 1974), 20 to 100% (Webb, 1977), 20 to 30% (Crossley, 1977).

A large proportion of the necromass consumed by saprophages is egested and is degraded by the microflora. The latter account for the major part of energy flow through soil biota, with fungi being the most important group of decomposers (Satchell, 1971; Swift et al., 1979). According to a rough approximation, soil and litter animals respire 10% of litter input, and the microflora metabolizes 90%.

Predators

Some studies demonstrate high predation pressures in forest canopy and in the litter–soil subsystem (Edwards et al., 1981; Schaefer, 1983; Grimm and Funke, 1986). Horstmann (1982) found that the ant *Formica polyctena* may have consumption rates up to 400 kJ m^{-2} yr^{-1} in a German oak (*Quercus robur*)–hornbeam (*Carpinus betulus*) forest.

NUTRIENT CYCLES

The cycling of elements is a basic property of ecosystems, and has been developed as a concept of modern ecology (Bormann and Likens, 1981). What is the function of animals in affecting and completing the nutrient cycle?

Nutrient cycling is essentially a polycyclic phenomenon (Spurr and Barnes, 1980). It consists of three major cycles: the external geological cycle of nutrient inputs from the atmosphere, geological weathering of parent material and losses through leaching; the biological cycle of plant–soil exchanges, with participation of the fauna; and the within-tree cycle of uptake and translocation.

Nitrogen, phosphorus, potassium and calcium are the chemicals most often in short supply in the soil. Nitrogen and phosphorus are limiting elements, potassium, calcium, magnesium and sulphur are in most cases non-limiting among the elements essential for plants, sodium is non-essential. Among essential plant nutrients, nitrogen, phosphorus and sulphur are more dependent on biological modes of replacement (Swift et al., 1979). According to a model of decomposition developed by Smith (1979), the annual-average soil solution concentrations of phosphorus and potassium are independent of the soil biota activity, in contrast to the various forms of nitrogen. Only nitrogen is likely to limit primary production in unfertilized oak and beech forests (Vitousek et al., 1979). Recently it has been recognized that phosphorus may be limiting for microfloral populations in the soil, and thus may control mineralization rates (K.H. Domsch and M. Vanselow, pers. comm., 1986; Scheu, 1987).

Animals may act as immobilizers (incorporating elements into their tissue); as accumulators (concentrating elements in their body); and as transfer agents (channelling elements to the compartment "dead organic matter" via egesta and dead zoomass), providing the microflora with elements, which can be mobilized within a short time (Fig. 9.9). Additionally, animals influence nutrient fluxes indirectly, mainly by comminution of plant and litter material and by interaction with the soil microflora (see p. 194).

In studies of the roles of particular organisms in chemical cycling, it is essential to know the element content of the organisms and their food. Such data, together with biomass estimates and rates of chemical turnover, can be used to describe chemical flux by the consumer organisms (Carter and Cragg, 1976). Existing studies do not provide an

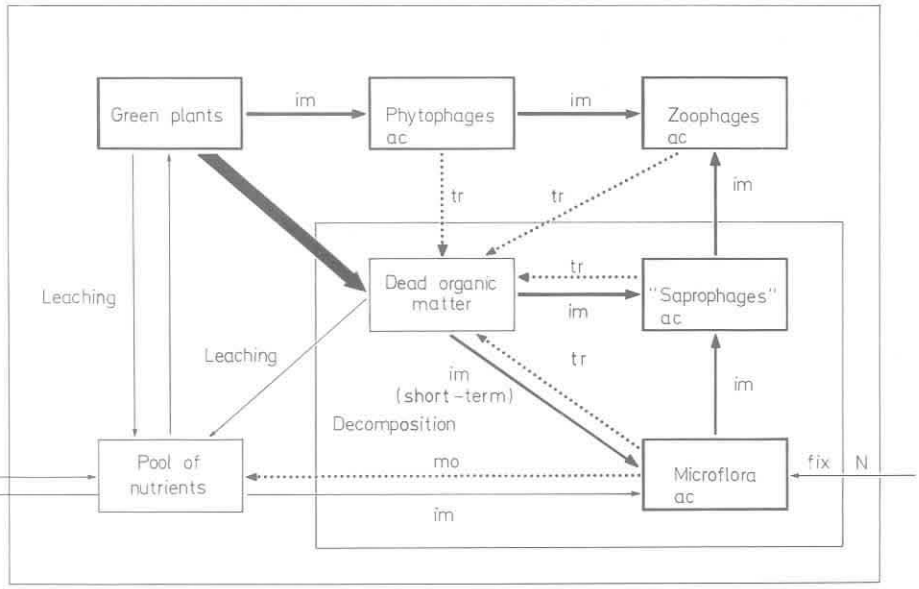

Fig. 9.9. Diagrammatic representation of the function of animals in nutrient cycling as accumulators, immobilizers, transfer agents and mobilizers. ac = accumulation, im = immobilization, tr = transfer, mo = mobilization.

overall picture of the function of animals in nutrient flux patterns. Therefore I will present only a few examples in the following paragraphs.

Nitrogen

Nitrogen fixation due to the activity of microorganisms probably plays only a minor role in the nitrogen cycle of most ecosystems. Data are not reported for the I.B.P. woodland sites (Ulrich et al., 1981). However, Remacle (1971) states that many nitrogen-fixing species of *Pseudomonas* are recorded in forest soils, and he observed nitrogen accumulation in incubated litter. Swank and Waide (1979) reported an annual rate of nitrogen fixation of 1.204 g N m^{-2} yr^{-1} for an undisturbed North American oak–hickory forest. Likens et al. (1977) give a value of 1.4 g N m^{-2} yr^{-1} for a North American hardwood forest.

Nitrogen is efficiently retained and recycled, as was demonstrated by Mitchell et al. (1975) for a mature North American hardwood forest. However, only 3.6% of total nitrogen was localized in forest biota. The authors calculated an output of 2.29 g N m^{-2} yr^{-1} by the soil fauna, whereas the microflora remineralized annually 12.4 g nitrate nitrogen and 28.2 g ammonium nitrogen per square metre. In a North American *Liriodendron tulipifera* forest 14.07 g N m^{-2} yr^{-1} passed through the decomposer food web (McBrayer, 1977). Invertebrate production represented 900% of the nitrogen in litter consumed by the animals because fungi being rich in nitrogen were the primary source of nitrogen for the animals. Production of decomposer invertebrates (4.68 g m^{-2}) is equivalent to 70% of the nitrogen released during litter decomposition and represents a quickly mobilized form of ammonium (McBrayer, 1977).

Soil animals may play a role in regulating nitrogen mineralization in three ways: by faunal grazing (Anderson and Ineson, 1983); by influencing resource utilization by the microflora; and by excretion of significant amounts of simple nitrogenous compounds, such as urea, uric acid and ammonia. Earthworms may constitute a rapidly utilizable pool of nitrogen. It has been calculated that 10% of the nitrogen remineralized in forest soils during one year may originate from earthworm tissue, excretion and mucus production (Lakhani and Satchell, 1970). Additionally, earthworms stimulate microbial mineralization of nitrogen by the production of faeces (Scheu, 1987).

Bosatta and Staaf (1982) have presented a "semi-empirical" model for describing the nitrogen dynamics of decomposing forest litter in a medium-long time perspective. Results from simu-

lations indicate the strong regulating influence of decomposition rate (which is, among other factors, controlled by animals) and initial nitrogen concentration of the litter on the retention and release of nitrogen by the litter. An increased decomposition rate tends to reduce the rate of nitrogen release per unit carbon mineralized. This makes the "critical" C/N ratio of a litter, below which net nitrogen mineralization takes place, lower the higher the decomposition rate. For a litter of low initial nitrogen concentration, a faster decomposition rate generally also means a greater amount of nitrogen immobilized, but a shortened immobilization phase. The peak of mineralized nitrogen is more marked and comes earlier the lower the C/N ratio and the higher the decomposition rate.

Phosphorus

Phosphorus analyses of soil invertebrates (Enchytraeidae, Dorylaimidae and Elateridae) in a Canadian grassland indicated that, of the total phosphorus in the invertebrate tissue, less than half is present in organic form. Hence the role of these animals in phosphorus transformations seems to be relatively more important than their biomass indicates (McKercher et al., 1979). The soil invertebrate biomass in the grassland was about 10% of the bacterial biomass, but could contribute 30% to the labile phosphorus pool during the winter study period. This observation explains why the phosphorus in arthropod remains is lost more rapidly than in the leaf litter (Seastedt and Tate, 1981). Cole et al. (1978) demonstrated that soil amoebae mineralize phosphorus retained in bacterial biomass and return it to the inorganic nutrient pool. However, nematode effects on phosphorus mineralization were small.

In a North American *Liriodendron* forest, soil and litter invertebrates processed 1.87 g P m^{-2} yr^{-1} (McBrayer, 1977). Total annual production of invertebrates utilizes the equivalent of 118% of the phosphorus contained in litter-fall. Obviously, phosphorus is conserved in the animal component by internal cycling.

Sulphur

In contrast to the nitrogen cycle, the sulphur cycle is not, or only to a small extent, controlled by biotic influences. Sulphur supplies in a North American hardwood forest (Tennessee) are abundant. Sulphur accumulates mostly by inorganic, chemical immobilization in the soil — that is, by geochemical processes (Johnson et al., 1982). Soil and litter animals in a North American *Liriodendron* forest required only 13.7% of the sulphur in litter-fall for production (McBrayer, 1977). The faeces of the isopod *Oniscus asellus* had higher concentrations of sulphur than its food, leaves of *Acer negundo* (Mitchell et al., 1983). This was probably due to the microbial conversion of inorganic sulphate to microbial products by assimilatory sulphate reduction. Thus, isopods accelerate the conversion of inorganic sulphur to organic forms.

Calcium

The calcium content of the canopy increases during the vegetation period; leaf litter introduces this element into the litter–soil subsystem. Some litter grazers have high calcium concentrations, particularly diplopods, isopods and oribatid mites (Swift et al., 1979). In a Canadian aspen (*Populus tremuloides*) wood, most arthropods had calcium concentrations ranging from 1.1 to 2.1 mg g^{-1} dry wt, with a maximum of 108.4 mg g^{-1} for stratiomyid larvae and millipedes, both with highly calcareous exoskeletons (Carter and Cragg, 1976). For a population of *Eupterotegaeus rostratus* Carter and Cragg (1977) observed a small amount of ingestion (0.122 mg m^{-2} $month^{-1}$), in comparison to an annual calcium input of 3.15×10^3 mg m^{-2}. The standing crop of this oribatid population was 0.130 mg m^{-2}. However, adults of *E. rostratus* accounted for only 0.4% of the total adult oribatids in the aspen (*Populus tremuloides*) forest soil. All the adult carabids of this forest recycled only 0.1 mg Ca m^{-2} during the main period of reproductive activity (Cragg et al., 1977). In a southeastern hardwood forest in Georgia (U.S.A.), 12% of the annual calcium input to the soil originated from the "saprophages" (Gist and Crossley, 1975b). Of the calcium input by leaf litter, 11% was processed by the litter animals in a hardwood watershed in North Carolina (U.S.A.) (Cornaby et al., 1975). In a North American *Liriodendron* forest, 11.03 g Ca m^{-2} yr^{-1} passed through the

decomposer food web, but only 0.98 (8.8%) was directly from litter (McBrayer, 1977).

Fungi may accumulate calcium (Cromack et al., 1979; Beck, 1983). Crystals of weddellite and whewellite, calcium salts of oxalic acid, adhere to the outer surfaces of fungal hyphae in the litter layer of forest soils (Graustein et al., 1977). The presence of oxalate in soil solution speeds the weathering of soil minerals and increases the availability of nutrients to vegetation. The chelation of iron and aluminium keeps phosphorus available to plant roots, since phosphorus is scavenged from solution by the precipitation of iron and aluminium as hydroxides. Oxalate produced by fungi is commonly a component of soil solutions. Production of oxalate serves to retain calcium in the rooting zone.

Seastedt and Tate (1981) observed long half-lives of calcium (and magnesium) in arthropod remains in comparison to phosphorus; thus, mobilization of calcium is slow.

Potassium

Potassium concentrations tend to decrease in the canopy during the vegetation period. This was observed by Cragg et al. (1977) for aspen (*Populus tremuloides*) leaves in a Canadian forest. Potassium is released very quickly from freshly fallen litter (Swift et al., 1979). Its rate of release is mainly dependent upon the percolation rate of soil water passing through the humus layer (Ulrich et al., 1981).

In a south eastern hardwood forest in Georgia (U.S.A.), the saprophages accounted for only 1% of the total potassium flux from the litter compartment (Gist and Crossley, 1975b). For a hardwood forest in North Carolina (U.S.A.) this value was 3% (Cornaby et al., 1975).

All consumers in an aspen (*Populus tremuloides*) forest concentrated potassium (and sodium) over the concentrations found in living leaves, the fermentation layer and in fungal mycelia (Carter and Cragg, 1976). In this forest, potassium levels in arthropods were highest in lepidopteran larvae with 33.5 mg g^{-1} dry wt. The amount ingested by the oribatid *Eupterotegaeus rostratus* in this forest was small (0.008 mg m^{-2} $month^{-1}$ during peak feeding from mid-May to mid-July) in comparison to an annual input of potassium through leaf litter-fall of 0.96×10^3 mg m^{-2}. Standing crop of potassium was only 0.032 mg m^{-2} in *E. rostratus* populations (Carter and Cragg, 1977). In this forest the total adult carabids recycled only 2.5 mg K m^{-2} during the main period of reproductive activity (Cragg et al., 1977).

Function of animals in forest nutrient cycling: an evaluation

Saprophages have a direct and indirect influence on nutrient release and immobilization in litter and soil (Swift et al., 1979), and are an integral part of nutrient flux. Microcosm studies demonstrated that animals (Enchytraeidae, Collembola, millipedes and lumbricid worms) enhance release of elements (sodium, potassium, calcium and mineral nitrogen) from oak leaf litter (Anderson et al., 1983a, 1983b). According to McBrayer (1977), there is evidence that the invertebrates of a *Liriodendron tulipifera* forest are important for mobilization rates of nitrogen and phosphorus, but that they have no direct effect on release rates for essential cations (calcium, magnesium, potassium). Litter-bag experiments demonstrated that microarthropods increase losses of nutrients (calcium, potassium, magnesium and phosphorus) from forest litter by comminution (Seastedt and Crossley, 1980; Seastedt, 1984); however, microbial stimulation as a result of microarthropod feeding activities appears to increase the nutrient-retention capacities of forest litter. Many animal groups in the soil–litter subsystem are not important in nutrient dynamics from the point of view of participation in these fluxes. However, species may be important as regulators, by governing or controlling flux patterns or rates.

The role of phytophages in forest nutrient fluxes is more difficult to interpret. Insect herbivores have been shown to influence nutrient flows by: (1) stimulating net primary production and nutrient uptake in moderately grazed plants; (2) increasing translocation of nutrients from plant reserves to sites of insect grazing; (3) increasing mass and nutrient content of litter-fall during the growing season; (4) increasing leaching of foliar nutrients from chewed leaves; (5) stimulating (via nutrient-rich leachates, litter fall and faeces) nitrification, nitrogen-fixation, litter decomposition and/or root growth rates within the litter–soil complex; and (6)

altering long- and short-term nutrient cycling pathways through changes in the relative biomass of canopy and subcanopy plant species (Springett, 1978; Owen, 1980; Schowalter, 1981; Schowalter et al., 1981).

The importance of these herbivore effects on the nutrient cycles of the whole forest ecosystem has yet to be investigated. According to Schowalter et al. (1981), forest insect herbivores in clearcut and undisturbed forests consumed an estimated 300% of foliar standing stock of sodium, 30% of potassium and 2 to 5% of calcium and magnesium during the growing season. A population of the aphid *Macrosiphum liriodendri* on *Liriodendron* trees consumed 17% of the annual standing crop of foliar nitrogen (Van Hook et al., 1980). Insect consumption in the canopy may elevate concentrations in the through-fall. Principal mechanisms are increased leaching from damaged leaves; and increased fall of litter, frass, insect exuviae and exudates such as honeydew (Parker, 1983). Seastedt et al. (1983) found that through-fall concentrations of ammonium, phosphate and sulphate under individual black locust (*Robinia pseudoacacia*) and red maple (*Acer rubrum*) trees were significantly related to the percentage of canopy consumed by insects. On the average, over 0.7 g of nitrogen, almost 0.6 g of potassium, over 0.2 g of phosphorus, and almost 5.2 g of calcium are deposited annually per square metre in a Polish oak (*Quercus robur*)–hornbeam (*Carpinus betulus*) forest (Witkowski and Borusiewicz, 1984). Thus phytophagous insects have been postulated to act as regulators of nutrient cycling (Mattson and Addy, 1975; Petrusewicz and Grodzinski, 1975; Kitchell et al., 1979).

ANIMALS AS HETEROTROPHIC REGULATORS IN FOREST ECOSYSTEMS

Ecosystem persistence

Persistence is a basic property of deciduous forest ecosystems. This refers to the structure and organization of the system, as well as to energy flow or nutrient flux patterns. At least three components are needed to explain ecosystem persistence (Reichle et al., 1975; O'Neill, 1976; O'Neill and Reichle, 1979): producers, heterotrophs as rate regulators, and a large storage component with slow turnover.

It is self-evident that the autotroph populations could exhaust available element resources, resulting in collapse of the energy base, unless heterotrophs regulate the rate of autotrophic processes (Reichle et al., 1975).

According to a hypothesis of O'Neill and DeAngelis (1981), the amount of soil organic matter plus wood tissue per gram of active leaf tissue should increase as climatic factors become more favourable. As turnover times increase, the heterotroph/autotroph ratio decreases. The more rapid the turnover of the system, the greater the heterotroph biomass required to maintain and regulate energy flow through the system.

For animals as regulators, one has to look for a "multiplier effect" on some ecosystem processes, out of proportion to the size of the action *per se* (Chew, 1974). This is a situation with a high energy quality ratio — that is, where the amount of energy flow controlled by an action (="information flow") is high in relation to the energy of the action itself. This includes, for instance, bark consumption leading to the girdling of trees, seed predation, feeding by key-stone predators, competition, digging. Important information flows leading to rate regulation by heterotrophs are represented in Fig. 9.10: they include consumption of living plant material, processing of dead organic matter by "saprophages" and microflora, and mineralization by microflora.

Role of herbivores

Because consumption in forest canopies may be only a few percent of NPP, the impact on photosynthetic potential can be nil, since the plant is capable of compensating for loss of green material. On the other hand, there are indications that phytophages may affect primary production by influencing the whole metabolism of the tree. The main impact (and regulatory influence) of herbivorous insects, especially defoliators, appears to be increased loss of elements (such as nitrogen) favouring leaf instead of wood production, which increases litter turnover rates and accelerates the rates of recycling of labile elements in the litter–soil horizons (Swank et al., 1981). However, this hypothesized effect has not been quantified. Ac-

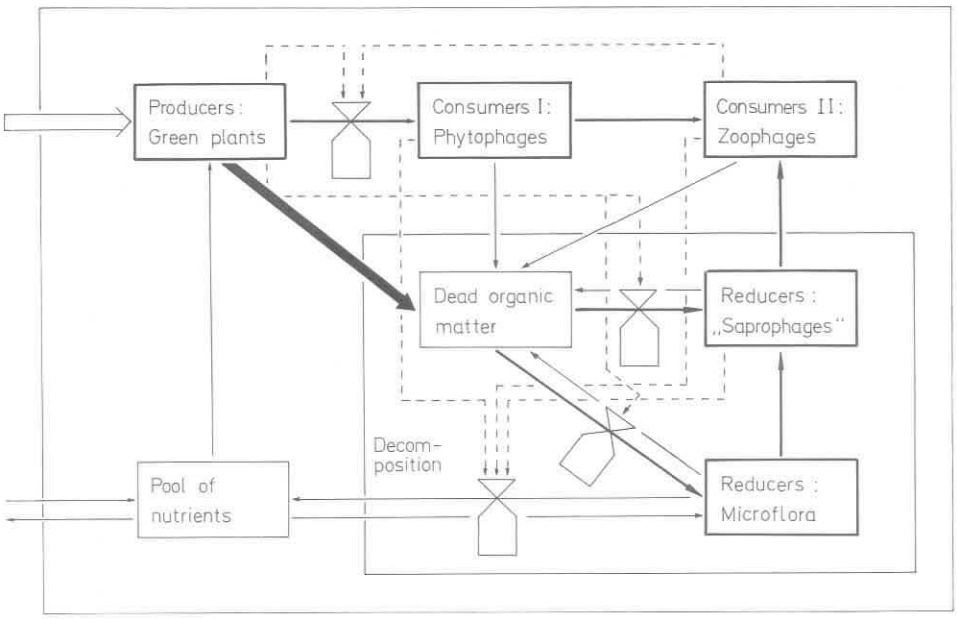

Fig. 9.10. Diagrammatic representation of rate regulation in forest ecosystem. Hatched lines indicate information flows. Further explanation in Fig. 9.1.

cording to Matekin and Ugolkova (1979), the acceleration of cycling of material by comminution of the plant biomass by phytophages leads only to about 1% of new primary production. In many cases the effect of added herbivore faeces, biomass, frass or exuviae on litter turnover rates is imperceptible. On poor sandy soils the addition of organic matter would result in an increase of the cation exchange capacity of the soil; that is, the soil would be able to retain nutrients more effectively. In addition, the water-holding capacity of the soil would increase (Petelle, 1981). Release of sugar by aphids (such as *Eucallipterus tiliae*) may increase the rate of nitrogen fixation by bacteria and thus affect the fertility of the soil. The presence of phytophages lengthens the season of leaf fall; thus, leaf fall is less concentrated in one specific season of the year (Owen and Wiegert, 1976).

Consumption of roots, in addition to sloughing, may facilitate the invasion of new areas of the soil by the root system (Harris et al., 1979).

Digging by herbivorous mammals may contribute to "pumping" of soluble nutrients from the deeper soil layers onto the surface, and the movement of insoluble materials to the surface, where they are weathered (Golley et al., 1975).

Role of decomposers (saprovores and grazers)

Heterotrophic effects are greatest in decomposer processes. In a forest ecosystem about 90 to 95% of total heterotrophic respiration is contributed by decomposers (see p. 200). The heterotrophic community performs an important function in controlling the fluctuations in the rate of release of nutrients.

In the decomposer food web, the amount of litter material processed by saprophagous populations may depend upon the input. For instance, Stachurski (1974) found higher biomass values, consumption and defaecation rates of the isopod *Ligidium hypnorum* in patches with a higher amount of accumulated leaves. Arguing in a similar way, McBrayer et al. (1977) suggested that litter production determines microarthropod densities. However, Harding and Stuttard (1974) noted that microarthropod densities increase with increasing latitude; hence, densities are correlated with standing crops of organic matter and not with litter production (Seastedt and Crossley, 1981; Petersen and Luxton, 1982). Generally the litter–soil subsystem is capable of processing the amount of litter produced, though with different turnover rates.

The disturbance of a soil community leads to rapid decomposition and mineral leaching (Reichle, 1977). It would appear that, under undisturbed conditions, the presence of microarthropods grazing upon microflora "regulates" the rate of decomposition, so that a more linear release occurs throughout the growing season. Soil animals immobilize nutrients within their tissues for extended periods of time (Luxton, 1979). In the context of the ecosystem, a controlled, continuous release of nutrients from detritus versus a rapid loss and flux from the system is advantageous.

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